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Hydrographical and Biological Conditions in the North Sea as Indicated by Plankton Organisms.

By

F. S. Russell.

Introduction.

FROM the beginning of the investigations of the International Council for the Exploration of the Sea the possibility of using plankton organisms as indicators (Leitformen) of water movements has been constantly borne in mind. This idea had already been suggested earlier by Cleve and Aurivillius, and was probably in the minds of most plankton workers, for when the habits of plankton organisms are known these organisms form ideal drift-bottles.

In the present review of the research on plankton indicators I shall restrict myself chiefly to work done in the North Sea area since the war, a brief historical survey having already been given previously (Russell, 1935 b, p. 13). It will be sufficient here to give the references to the publications of earlier workers such as those of Gran (1902), Gough (1905 a and b), Damas and Koefoed (1907), Ostenfeld (1908) and Bygrave (1911). In addition there is much important information to be found in the comprehensive *Bulletins Planktoniques* of the International Council.

But from the start it was fully realized that the problem could not be tackled satisfactorily until the full distribution of all species was worked out and until more was known about the life histories of the animals. Thanks to the co-operative work of the International Council and to the researches of individual workers both these aspects have received considerable attention. As a result the study of plankton indicators has shown a marked advance in recent years.

In the post-war period the first publications bearing on the use of plankton indicators were those of Bowman (1923 a and b), who instigated the study in Scottish waters, and of Hardy (1923) on the occurrence of certain plankton species off the east coast of England during the unusual hydrographical conditions of the year 1921.

In 1927 Kramp published his comprehensive work on the Hydromedusae of Danish waters, followed in 1930 by a paper on the Hydromedusae in the south-western part of the North Sea and the eastern part of the English Channel. Both these publications had as a major aim the association of the distribution of the Medusae with the movement of the water masses.

Meek (1928), by a study of the *Sagitta* population off the Northumberland coast, was the first to show that an examination of the relative abundance of the two species, *Sagitta elegans* and *S. setosa,* might produce valuable indications of hydrographical conditions.

Meanwhile Savage (1930), with his publication on the influence of *Phaeocystis* on the migrations of the herring, produced data which were to the followed by the important works on the distribution of phytoplankton patches in the southern North Sea, in collaboration with Hardy (1935) and with Wimpenny (1936). This work introduced a somewhat different type of observation in that the movements of whole patches of diatoms, chiefly *Rhizosolenia styliformis* and *Biddulphia sinensis,* were followed in successive years from 1921 onwards.

Wulff and Künne (1933), sponsored by Mielck, completed observations in the southern North Sea, which showed the relationships of both the microplankton and the larger plankton animals to the hydrographical conditions in that area.

At about the same time observations made at Plymouth and off the western end of the English Channel (Russell, 1935 a, 1936) showed the importance of certain of the larger plankton animals as indicators, and carried Meek's work on *Sagitta* a stage further. This was followed, in a review of zooplankton research (Russell, 1935 b) by remarks on the value of this type of work and a list of animals likely to be of use in different areas, compiled from the observations of earlier and recent workers.

Since that date further important works on certain indicator species have been published. Künne (1937 a) followed up his earlier research with a paper on the indicators in the southern North Sea in winter and also (1937 b) in the Baltic. In the latter paper Künne gives lists of those species which can be regarded as visitors (Fremdlinge) to the different regions of the Baltic.

Fraser (1938 and 1939) has given data on the distribution of Chaetognatha, including *Sagitta elegans* and *S. setosa,* and of other plankton animals in the northern North Sea and Scottish waters; and Furnestin (1938) compared the distributions of species of *Sagitta* with the salinity in the whole North Sea area.

During this period a number of shorter notes had been published on the occurrence of certain organisms which might prove of value as indicators in different areas; Russell and Kemp (1932) on *Velella* and *Ianthina* south-west of the British Isles; Lucas (1933) on *Dolioletta gegenbauri* in the northern North Sea; Russell and Hastings (1933) on the occurrence of salps and doliolids in the

English Channel; Russell (1934) on the siphonophores *Muggiaea atlantica* and *M. kochi* in the western end of the Channel; and Beatson, Nicol and Elton (1936) on *Ianthina, Velella* and *Lepas* on the west coast of Scotland. In addition a number of valuable notes are to be found in the annual reports of the Fishery Board for Scotland.

This list of workers would not be complete without mention of the work of A. C. Hardy and his collaborators[1]) on the distribution of plankton studied by means of his continuous recorder and the indicator disks supplied to fishermen. For it seems probable that Hardy's continuous recorder will prove to be one of the most valuable means of obtaining a broad picture of the distribution of indicator organisms over the whole area. As a result of this more recent work we are now in a position to differentiate more clearly between a number of plankton communities which typify the water masses in which they occur. Furthermore these water masses or "types of water" usually differ one from the other in origin or immediate past history, in so far as their salt content and temperature allow their more immediate origin to be deduced. Our knowledge of the different areas will be outlined below, and a resulting generalized picture drawn of the conditions over the whole North Sea area.

I have limited myself as much as possible to literature mainly concerned with plankton indicators, and have omitted detailed reference to hydrographical work as this would have unduly lengthened the list of literature. Much help has, however, been obtained by a study of the hydrographical publications, and among the works especially consulted are those of J. N. Carruthers, H. W. Harvey, J. R. Lumby, D. J. Matthews, and J. B. Tait. It may appear, perhaps, that I have over-simplified the story. The complexity of the water circulation must be fully realized, but in so short an account the qualifications necessary in describing any one area would have destroyed the clarity of the picture.

The Indicators for Different Areas.

Southern North Sea.

The following "types of water" are recognized in this area (see Fig. 1).

1. Northern water, brought into the area from the north, and especially from the north-west. This water is drawn from mixed oceanic and coastal water from the north, which is reduced in the southern North Sea to a salinity less than 35 ‰. It goes partly into the south-west Dogger Bank swirl, and also in part southwards along the east coast of England, turning finally in an easterly direction.

The northerly elements of the plankton which are indicators of the presence of this northern water are (Künne, 1937 a):—

[1]) Marshall, N. B. North Sea plankton recorder survey, 1938: Zooplankton other than Copepoda. Hull Bull. Marine Ecol. (In the press).

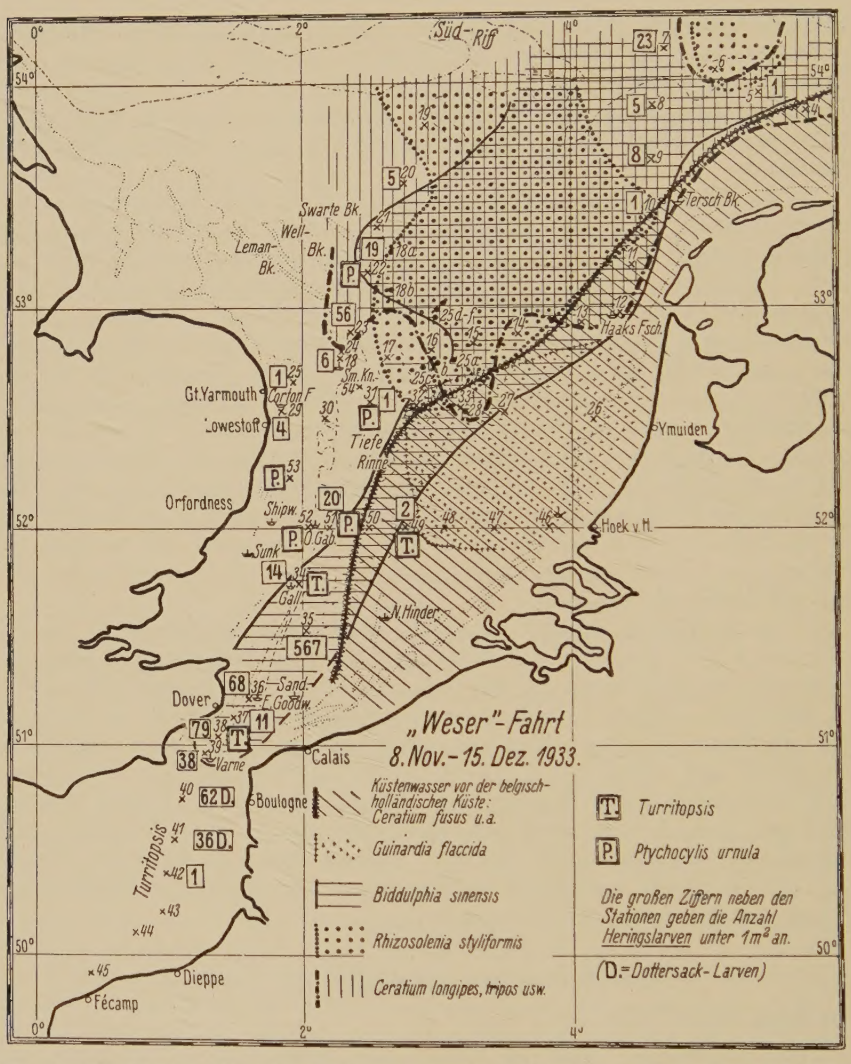

Fig. 1. Distribution of microplankton in southern North Sea. (From W u l f f, 1933).

Hydromedusae: *Tima bairdi, Cosmetira*[2]), *Aglantha*[2]), and the siphonophore *Agalma elegans.*
Chaetognatha: *Sagitta elegans elegans.*

[2]) *Turritopsis, Cosmetira,* and *Aglantha* are here designated by generic names only. K ü n n e identifies the first two as *Turritopsis polycirrha* Keferstein and *Cosmetira megalotis* (Maas). They are probably synonymous with *Cosmetira pilosella* Forbes and *Turritopsis nutricula* McCrady, (see R u s s e l l, 1938). *Aglantha* in the area under discussion is the small form known by some as *A. digitalis* f. *rosea* and by others as *A. rosea;* they are the same Medusa.

Crustacea: the euphausians *Nyctiphanes couchi, Thysanoessa gregaria,* and other species, and the amphipod *Themisto abyssorum* (= *Parathemisto oblivia*).
Pteropods: *Clione limacina* and *Limacina retroversa.*
Echinoderms: *Luidia sarsi* larvae.
Appendicularia: *Oikopleura labradoriensis.*

2. Channel water, entering the southern North Sea through the Straits of Dover. It may be composed of pure Channel water, or of mixed oceanic and coastal water from the western mouth of the Channel. Both these waters may become mixed together in the Dover Straits region. The water may reach a salinity of 35 ‰ or more. It passes north-east towards the Jutland coast.

The indicators of Channel water are:—

I) Pure Channel water.
Microplankton (Wulff, 1933): *Biddulphia sinensis.*
Macroplankton (Künne, 1937 a).
Hydromedusae: *Turritopsis*[2]) and *Gossea corynetes.*
Mollusca: *Lamellaria perspicua* larvae.

II) Mixed oceanic and coastal water (see English Channel and South Ireland area below).

3. Flemish coast water, occurring along the Belgian and Dutch coasts. It becomes mixed along its offshore boundary with Channel water and moves in a north-easterly direction along the Jutland coast.

The indicators of this water are:—

Microplankton (Wulff, 1933): *Paralia sulcata,* small *Coscinodiscus, Bellarochea malleus, Guinardia flaccida, Thalassiothrix nitzschioides, Ceratium fusus* and *Ceratium furca.*
Macroplankton (Künne, 1937 a): the pelagic hydroid *Clytia*[3]). This water is also notable for the amount of detritus it carries.

4. Remaining coastal waters, found close into the coasts along the east coast of England and the Belgian, German and Dutch coasts, especially in the regions of the river mouths. It has a low salinity and carries much detritus.

Its indicators are:—

Eastern English coast.
Microplankton (Wulff, 1933): *Biddulphia mobiliensis* f. *regia* and *Ptychocylis urnula.*
German Bight.
Macroplankton (Künne, 1937 a): the Medusa *Sarsia tubulosa.*

[3]) Künne uses the name *Clytia pelagica* for this hydroid. There seems to be little doubt that it is the same species as *Clytia johnstoni,* the hydroid of the Medusa *Phialidium hemisphaericum.* They are probably colonies regenerating in the plankton from fragments broken off from the sea bottom.

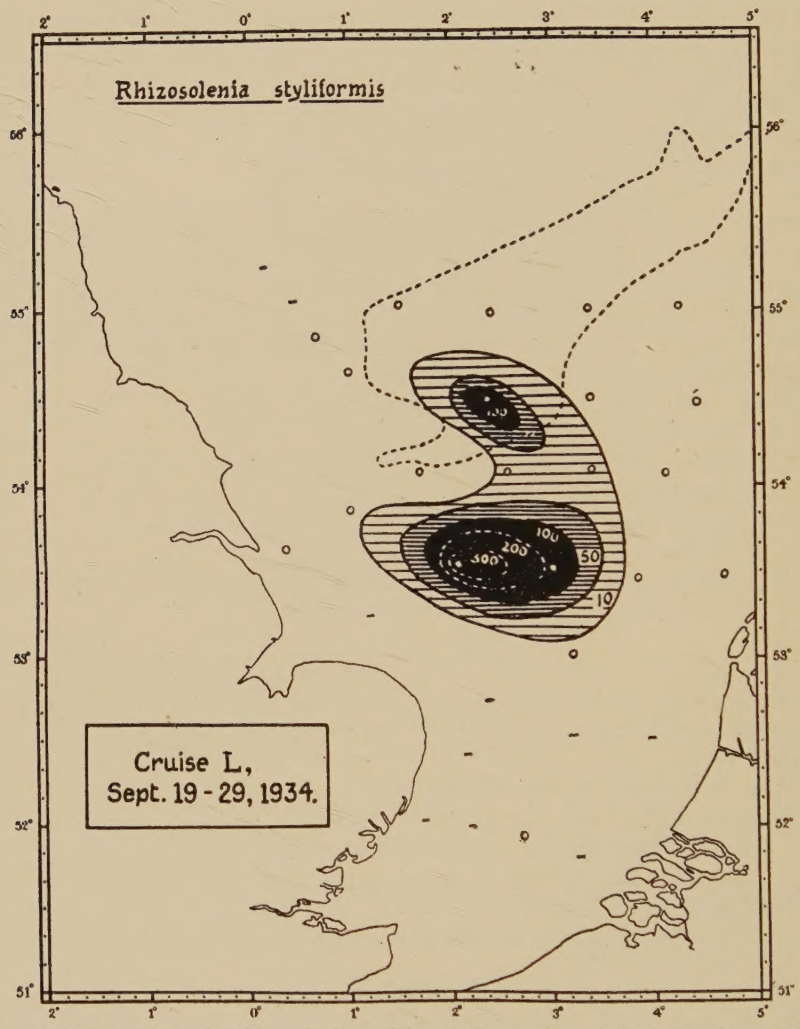

Fig. 2. Distribution of *Rhizosolenia styliformis* in southern North Sea in region of south-west Dogger Bank swirl; contoured in thousands of cells per cubic metre. (From Savage and Wimpenny, 1936).

5. Swirl waters. Most noteworthy in this region is the south-west Dogger Bank swirl (see Fig. 2).

It appears to draw its planktonic indicators entirely from the north, without admixture of Channel forms.

Its indicators are:—

Microplankton (Wulff, 1933): *Rhizosolenia styliformis, Ceratium longipes, C. macroceros, C. tripos* and *C. bucephalum.*

Macroplankton (Künne, 1937 a): those given above for northern water.

In considering the southern North Sea from the point of view of plankton distribution it must be realized that conditions are continually changing, as indeed they are in all areas. But perhaps in this area conditions are liable to more sudden alteration from effects of wind (e.g., Savage, 1932, on movements of *Pseudocalanus* swarms) and of outflow of fresh water from the land after heavy rainfall (e.g., Graham, 1938).

It is interesting to note here also that *Sagitta elegans* may occur in the Thames estuary (Wells, 1938).

Northern North Sea.

The information is taken from Fraser (1938, 1939).

1. Oceanic water entering in the extreme north through the Fair Isle Channel and mostly north of the Shetland Islands.

This water contains a mixture of warm and cold water species varying in their proportions according to the degree of influence of arctic water from the north and the Atlantic drift water from the south-west.

Among the indicator forms of this water are the following:—

I) Cold water.
Hydromedusae: the siphonophore *Dimophyes* (= *Diphyes*) *arctica.*
Chaetognatha: *Sagitta maxima* and *Eukrohnia hamata.*
Crustacea: the copepods *Calanus hyperboreus* and *Metridia longa.*
Pteropoda: *Limacina helicina.*

II) Warm water.
Hydromedusae: the siphonophores *Physophora hydrostatica, Agalma* (= *Agalmopsis*) *elegans* and *Galeolaria* (= *Galetta*) *truncata.*
Chaetognatha: *Sagitta serratodentata.*
Crustacea: the copepod *Rhincalanus nasutus* and several other species.
Pteropoda: *Clio pyramidata.*
Tunicata: various salps and doliolids.

2. Mixed oceanic and coastal water (see Fig. 3).
Hydromedusae: *Neoturris pileata, Laodicea undulata, Halopsis ocellata, Cosmetira, Tima bairdi,* and *Aglantha.*
Chaetognatha: *Sagitta elegans.*
Crustacea: the amphipod *Themisto.*
Pteropoda: *Limacina retroversa.*
This is a rich, often fatty, plankton, with abundant *Calanus finmarchicus.*

3. North Sea water. Its only indicator is:—
Chaetognatha: *Sagitta setosa.*
This plankton is usually not of a rich nature.

The sequence of events as we pass from north to south is as follows (Fraser, 1937, p. 313).

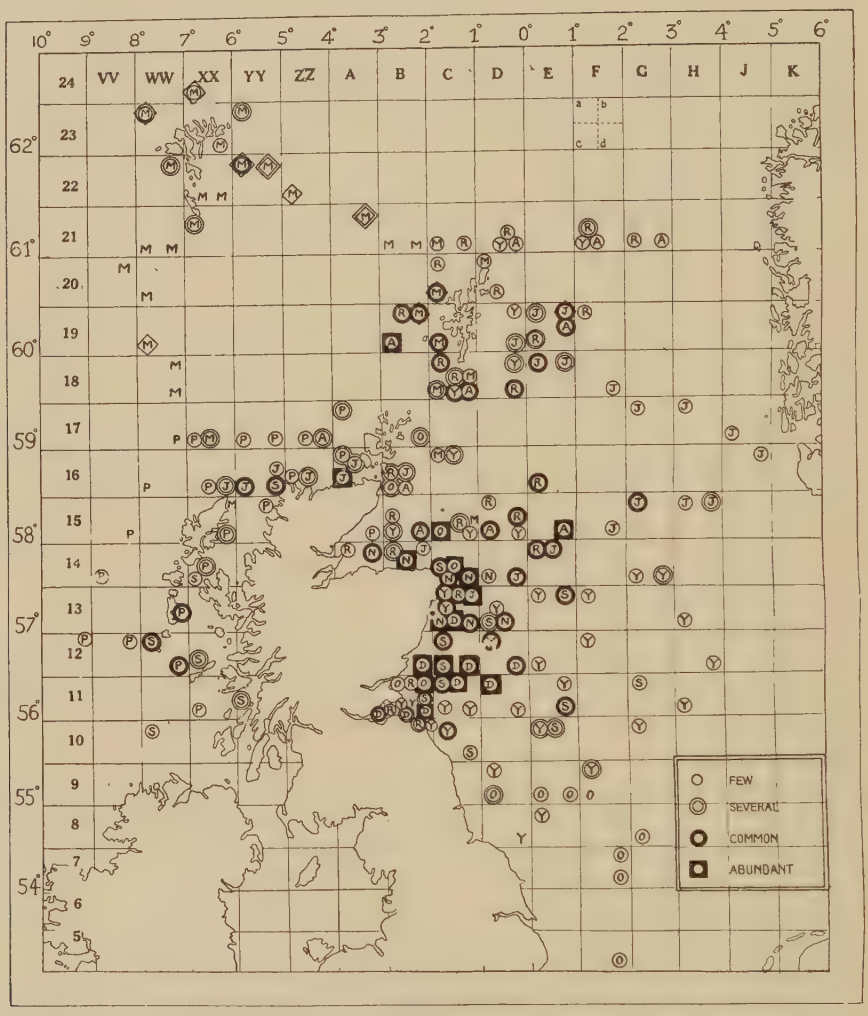

Fig. 3. The distribution of *Sagitta elegans elegans* (circles) and *S. elegans arctica* (diamonds) in Scottish waters in 1937. Letters indicate months. Unringed letters indicate absence of *Sagitta*. R. = March, P = Apr., M = May, J = June, Y = July, A = Aug., S = Sept., O = Oct., N = Nov., D = Dec. (From Fraser, 1939).

"As this mixed fauna moves round the north of Scotland the pure warm-water Atlantic forms gradually perish, but there is a further addition of arctic forms between Faroe and Shetland. These, too, gradually perish and the fauna is replaced by a growing admixture of coastal and neritic forms from the Scottish coasts, Shetland and Faroe, and this together with a probable replenishment from the Norwegian Deep south of 61°N. forms a very rich, often fatty, plankton with abundant *Sagitta elegans, Calanus finmarchicus*, and many Medusae.

Thus the fauna of the entering Atlantic stream becomes completely changed in quite a short space and time. In exceptionally favourable circumstances a few of the original forms persist and are carried into the North Sea as exotics, but as a rule only those forms which are capable of very rapid breeding (such as salps and doliolids in the asexual phase) are found in numbers in the North Sea."

Transition Area.

The Transition area is that region of the North Sea lying between the basin of the North Sea and the Baltic proper, comprising the Skagerak, Kattegat and Danish waters. It is a region of very marked hydrographic differences. The water masses involved are:—

1. Baltic water, of low salinity, flowing out as a surface layer and running north along the Norwegian coast.

2. Water of the Jutland current, entering the area in the deeper layers. This is formed of the mixtures of southern North Sea and coastal waters.

3. North Sea and oceanic waters entering in the deeper layers and varying in relative proportions.

The Medusa fauna of this area has been fully discussed by Kramp (1927). It is a very complex area and much experience in distinguishing the different plankton elements is required, since indications are mainly based on abundance or poverty of certain species. The more oceanic elements, however, such as the siphonophores *Physophora hydrostatica*, *Galeolaria truncata* and *Dimophyes arctica* are sufficiently obvious when they occur.

English Channel and Southern Ireland.

In this area the following types of water are recognized (Russell, 1936 b) (see Fig. 4).

1. Channel water, occupying the Channel proper. This water is characterized by a general paucity of plankton and its only indicators are:—

Hydromedusae: *Turritopsis.*
Chaetognatha: *Sagitta setosa.*

2. Mixed oceanic and coastal water, which forms a large swirl off the mouth of the Channel south of Ireland, and may at times be carried into the Channel. The indicators of this water are rather similar to those of the same type of water in the northern North Sea, but the more northern species are absent; they are:—

Hydromedusae: *Laodicea undulata, Cosmetira, Aglantha* and the siphonophores *Agalma elegans* and *Stephanomia bijuga.*
Chaetognatha: *Sagitta elegans.*

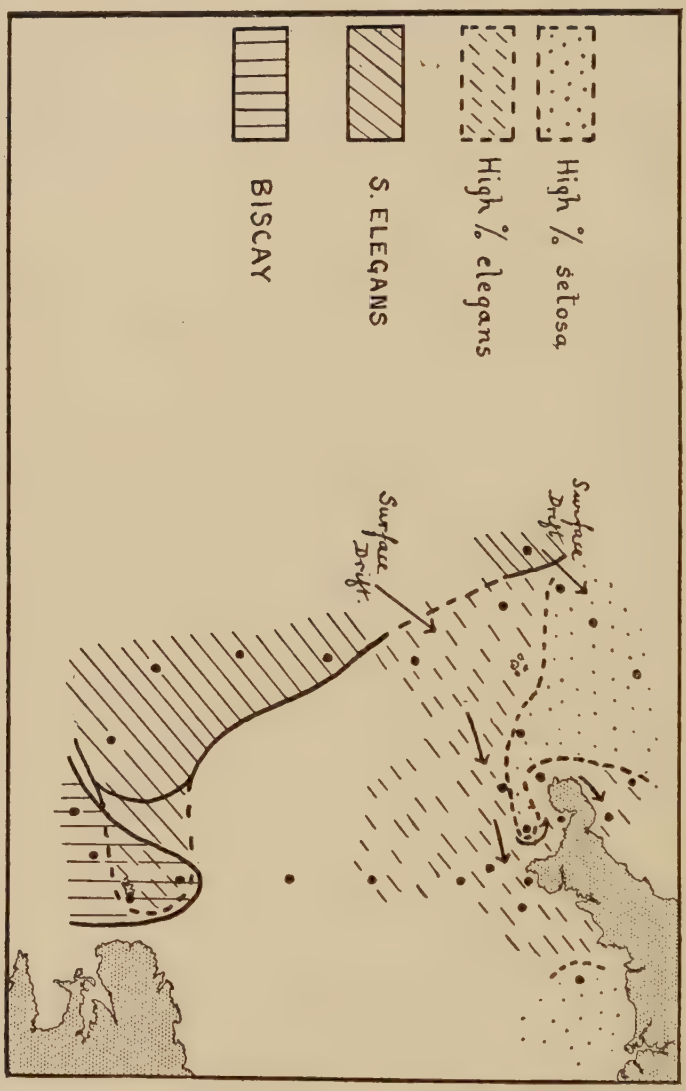

Fig. 4. Distribution of water masses in mouth of English Channel as shown by plankton collections in July, 1935. (From Russell, 1936 b).

Crustacea: the euphausians *Meganyctiphanes norvegica, Nyctiphanes couchi,* and *Thysanoessa inermis,* and the amphipod *Themisto gracilipes.*

Pteropods: *Clione* spp.

The plankton of this water is rich, and often of a fatty nature. The purely oceanic elements, as indicated by *Sagitta serratodentata* may occur mixed with the *S. elegans* plankton in proportions varying with the degree of oceanic influence. A mixed assembly of this plankton and the warm oceanic water species given below may also occur, similar to that described by Fraser for the northern North Sea.

3. Warm oceanic water, coming from a south-westerly direction; the indicators are:—

Hydromedusae: *Liriope tetraphylla* (= *exigua*), and (?) the siphonophores *Muggiaea atlantica* and *M. kochi.*
Crustacea: the copepod *Euchaeta hebes.*
Tunicata: various salps and doliolids.

In addition to the three types of water mentioned above there is possibly a fourth type. For several years water in the western end of the Channel has been characterized by a great number of pilchard eggs and a general poverty of plankton indicators, including both species of *Sagitta.* This water has been called provisionally "pilchard water" and the nature of the water has not yet been worked out.

The general principles of the circulation of water in the area are as follows:—

"Through oceanic circulation and wind effects there is a resultant flow of water through the Straits of Dover into the southern North Sea. The supply from which this water is ultimately drawn enters the mouth of the channel either from the west or south-west. It is generally conceded that more water enters the Channel than can pass through the Dover Straits, and this surplus probably drifts north-west or north past the Scillies—Land's End region, though the actual state of affairs here is not clear. To the west of the mouth of the Channel is a cyclonic swirl lying over the shallow continental plateau south of Ireland. This swirl varies in its extent and position; at times it appears to block the mouth of the Channel and at others apparently retreats farther north, thus laying the Channel mouth open to more oceanic water from the south and south-west. When there is a strong flow through the Dover Straits, water may move up Channel past Plymouth either from the swirl or from the ocean according to conditions existing off the Channel mouth. In the Channel itself there must be a body of water constantly being added to from the west and dissipated to the east, or hemmed into the coast to allow for passage of more oceanic water. The circulation of water in the Channel itself is clearly very variable from time to time." (Russell, 1938, p. 414).

It should also be mentioned that the water entering from the south-west may be of different types. Sometimes it is pure oceanic water; at others it may be coastal water of low salinity entering the Channel round Ushant (cf. Poole and Atkins, 1929).

Irish Sea and Western Coasts of British Isles.

Apart from the water flowing out from the rivers the Irish Sea draws its main supply of water from the complex existing off the mouth of the English Channel.

Its plankton appears to be mainly characterized by the *S. elegans* association. *S. setosa* occurs, however, in the Bristol Channel (Rees, 1939) and in the Morecombe Bay area[4]). Some *S. setosa* are probably carried out round the north of Ireland (Russell, 1935 a; Fraser,

[4]) E. L. Pierce — private communication.

Fig. 5. Generalized picture of the distribution of plankton in the North Sea area. The conditions shown are such as might be expected at one moment in the autumn of a year in which the influx of Atlantic water into the North Sea from the north was strong.

mixed oceanic and coastal water containing the *Sagitta elegans* plankton association. EL., *S. elegans:* RH. ST., *Rhizosolenia styliformis* in the south-west Dogger Bank swirl.

BID., Channel water with patch of *Biddulphia sinensis.*

Coastal waters; CL; *Clytia;* S. TUB., *Sarsia tubulosa* (in late winter and spring).

Oceanic water entering the Channel from the south-west.

The remaining area left white in the North Sea, Channel and Irish Sea is characterized by *Sagitta setosa;* SET., *S. setosa.* On the outer western edge of the *S. elegans* water is the pure oceanic water characterized by *Sagitta serratodentata* (SER.). The arrows indicate the general water circulation. It should be realized that there may in places be isolated patches of *S. setosa* water in the *S. elegans* areas.

1938); this species may also appear at times on the south coast of Ireland (Furnestin, 1938). It might also be expected to occur at places along the Welsh coast, since another associated indicator, *Turritopsis*, has been recorded from Tenby.

Along the outer western coasts of Ireland and Scotland, where the oceanic water comes in close to the coasts, the immediate coastal area carries a typical *S. elegans* community.

The North Sea Area as a whole.

With the information now available it is possible to construct a generalized picture of the distribution of plankton over the whole area. This I have attempted to do in Figure 5. The different types of water are inserted in this figure as they might be expected to be distributed at one moment in the autumn of a year in which the influx of Atlantic water into the North Sea from the north was strong. This figure is admittedly idealized and much simplified, but it is based fairly closely on the distribution shown in the different areas by the workers already cited. The general circulation of the water as shown by hydrographical observations has been indicated by arrows. The dependence of the plankton distribution on the general circulation of the water is at once obvious.

With such a diagram it becomes possible to visualize the picture as a whole and realize how changes going on in one area are linked with those in any other area.

The main points are that there is a large bay, the North Sea, containing water to which fresh water is added from the land and flowing out from the Baltic. At the same time the whole bay is open to the influx of water of oceanic origin from the north, and through a bottle-neck, the Straits of Dover, in the south. The surplus water flows out to the north. The so-to-speak resident plankton population of the North Sea water is characterized by *Sagitta setosa*, except in the coastal fringes of less saline water. The incursion of oceanic water gives rise to conditions in which a different plankton community, typified by *Sagitta elegans*, flourishes; and upon the extent of this incursion the variations in the configuration of the whole picture largely depend. Of first importance in this scheme is the fact that the mixture of oceanic water may produce a considerable enrichment of nutrient salts.

Although nutrient matter comes into the area off the land, e.g., the outflow from the Thames (Graham and Harding, 1938), there can be little doubt that the whole area is chiefly dependant for variations in its productive capacity on the extent of exchange with water from the north and south-west.

The far-reaching effects of this penetration are exemplified by the productive area of the south-west Dogger Bank swirl in almost the extreme southern part of the North Sea. This swirl is notable for the development at times of intensely thick patches of diatoms, especially

Rhizosolenia styliformis. The origin of the nutrient salts which give rise to this diatom growth has been examined by Graham (1938). His charts compared with those of Savage and Wimpenny (1936) slow clearly that in 1934 this region was provided with higher phosphate concentration during the summer than the rest of the area examined. The source of this phosphate is the northern part of the North Sea, the rich water passing through the "gateway" between the Doggerbank and Flamborough.

This conclusion appears also to be backed by plankton observations, the indicators in the south-west Dogger-Bank swirl being exclusively of northern origin (Künne, 1937 a). It is also supported by Wimpenny's (1937) observations on the plankton of the Flamborough region, for here *S. elegans* is in evidence and the crustacean plankton has a characteristically high fat content.

In order that the story may not appear too simple it will be as well to give further details of Graham's work. It was indicated that the Silver Pit was also a source of phosphate-rich water, apparently owing to regeneration of phosphate in the deeper layers during periods of temporary stability. Also, while the source of phosphate enrichment is to be traced to the northern North Sea Graham found that in the summer of 1936 large areas of the southern North Sea were well supplied with phosphate. Thus he concludes that apart from the Atlantic water there is an accumulation of phosphate beneath the thermoclines, the concentration of phosphate showing more relation to the thermocline than to the salinity.

It is reasonable, therefore, to suppose that a year of strong influx of rich Atlantic water may so enrich the area that its effects will be felt for several succeeding years. The heavy production of plankton made possible will, on death, give up a supply of nutrient salts to the deeper layers. In addition there may be an increased abundance of small bottom invertebrates due to successful survival of young in the rich year or even to the incursion of large numbers of larval stages with the rich water.

Graham also gave an indication that the stability of the *Rhizosolenia* patch may be related to rainfall and its influence on the outflow of fresh water from the Humber and perhaps the Wash. If this outflow is heavy the source of supply of rich water coming through the "gateway" is blocked, and the fresher water pushed into the swirl, leading to the cessation of diatom growth.

It seems reasonable to suppose that the degree of productivity in the whole North Sea area ultimately depends upon the amount of upwelling on the continental edge, which brings nutrient salts from the store in the deeper oceanic layers. It is thus self-evident that if at any time the main supply of water should be drawn from depleted surface oceanic waters, a poverty will ensue. This effect, also, as suggested above for rich water, may last for several years until the whole volume of water has been dissipated away into the ocean and replaced once more by richer water. In this connexion it must be

supposed that a considerable body of water may remain in one area for a long period of time in the form of an eddy or swirl. Otherwise it is difficult to account for the continued existence of a pure association of *S. elegans* plankton in such an area as that south of Ireland. Orton (1937) has drawn attention to the possibility of the importance of such areas for the settling of the larvae of bottom-living animals.

Plankton Indicators in Relation to Fishery Research.

With this general picture of plankton distribution in mind it is clear that the movements of rich or poor water may have far-reaching results on the fish population. On first thoughts we can realize that the plankton conditions may operate in two ways.

1. By influencing the survival of recently hatched young.
2. By causing the alteration of the routes of migrating fish.

The literature contains examples of both possibilities.

1. An example of the apparent effects of rich *S. elegans* and of poor *S. setosa* plankton is furnished by work at Plymouth.

For a number of years observations have been made at regular intervals on the phosphate content of the water, on the numbers of planktonic young fish, and on the changes in the *Sagitta* population. These results have been summarized by Russell (1936 b) and by Kemp (1938). They can be shown best in the following table which is that of Kemp, brought up to date.

Year	Phosphate in preceding winter % deviation from mean[1])	Young fish (less Clupeids)		*Sagitta*		
		summer spawners	spring spawners[2])	Total No. ÷1000	*S. elegans* %	*S. setosa* %
1924	+ 27	696	2133	—	—	—
1925	+ 9	140	1510	—	—	—
1926	+ 36	909	2051	—	—	—
1927	— 2	170	1014	—	—	—
1928	+ 23	—	—	—	—	—
1929	+ 23	321	502	—	—	—
1930	—	403	1114	91·5	94·1	5·9
1931	— 7	230	1395	117·3	16·7	83·3
1932	— 16	197	1359	118·3	6·2	93·8
1933	— 5	117	1220	117·4	4·7	95·3
1934	— 14	79	1065	94·5	3·5	96·5
1935	— 25	37	393	48·2	3·6	96·4
1936	— 16	115	372	24·0	39·7	60·3
1937	— 14	174	382	26·1	3·8	96·2
1938	— 16	135	315	20·4	1·5	98·5

[1]) Phosphate determinations made by Dr. W. R. G. Atkins and Dr. L. H. N. Cooper.

[2]) i.e., total young fish (less Clupeids) less summer spawners.

This table shows the correlation between the low numbers of young fish and the low phosphate content, coupled with the predominance of *S. setosa* off Plymouth. It is noticeable that the survival of the young of summer spawners was first affected.

2. The alteration of migration routes is best exemplified by the work of Hardy, Savage and Wimpenny on the influence of phytoplankton patches on the distribution of the herring shoals which give rise to the East Anglian fishery. These patches, which were chiefly *Rhizosolenia styliformis* or *Phaeocystis*, have been watched for a number of years, and they are an outstanding feature of the plankton in the area of the great herring shoaling. It was found that the position and intensity of these patches were apparently of great importance in the fishery, the landings being lowest in years of greatest concentration. On this evidence it was surmised that the dense phytoplankton has diverted the routes of shoaling fish.

Other indications of change in migration of herring which have not yet been confirmed are linked with the occurrence of *S. elegans* and *S. setosa*. E. Ford has followed the age composition of the herring shoals in the winter fishery off Plymouth for many years (for summary see Kemp, 1938). It has been a noteworthy feature that since 1931—2 there has been an absence of the younger year-classes of herring, the fishery in each successive year depending on an aging stock. As a result the fishery has now completely failed.

It is remarkable that just at the period of this change in the composition of the Plymouth herring population, a change took place in the composition of the *Sagitta* in the plankton. *S. elegans* gave way to *S. setosa* which has predominated ever since. There is a possibility that these herring results may be linked with other changes that have occurred in recent years. There have been indications of a northerly shift of the warm water fauna. At Plymouth the herring is near the southerly limit of its distribution, while the pilchard is on its northern limit. The occurrence of "Pilchard" water (see p. 181) off Plymouth may indicate that the herring have retreated farther north and the pilchard have taken their place.

We shall not be able to draw conclusions until the *S. elegans* conditions return once more off Plymouth, but it is perhaps significant that a similar herring-*Sagitta* correlation has been recorded off the Northumberland coast. Burton and Meek (1932) record that the herring fishery was poor in 1921 and 1926, in both of which years *S. setosa* was in evidence. It should, however, be noted that the herring off the Northumberland coast are feeding while those at Plymouth are spawning. The correlation with *Sagitta* off the Northumberland coast may therefore be accounted for by the large swarms of *Calanus* associated with *S. elegans* water.

In passing, it is interesting to note that the above authors also state that "There is a fairly definite positive agreement between the *S. setosa* periods and the Salmon catches of the Tyne".

These Northumberland observations deserve further comment, as

they show that the Atlantic influx into the North Sea may be of different types in different years (see, e.g., Storrow, 1939). It appears that in recent years the *S. elegans* water has been close in along the eastern coasts of Scotland and northern England, yet in 1921, in which year the Atlantic influx was so marked, *S. setosa* predominated on the Northumberland coast. It seems possible that the axis of influx was in that year more centrally placed in the North Sea so that the *S. setosa* water was forced into the coast and the north-flowing branch of *S. elegans* water was absent along the Northumberland coast.

There seems also to be an interesting connexion between the *Sagitta* population on the Northumberland coast and the distribution of salps in Scottish waters. I am most grateful to Mr. J. H. Fraser for the information on salps which is as yet unpublished[5]). In 1920 and 1925 salps were very abundant in Scottish waters, and in 1921 and 1926 they were also abundant though less so. In both the years 1921 and 1926 *S. setosa* was in evidence on the Northumberland coast. Mr. Fraser tells me that there were differences in the type of distribution of the salps in the north in these years. Both in 1920 and in 1925 an invasion of salps flooded the Moray Firth, but in 1921 and 1926 the Moray Firth was free of salps. These relations between the salps and *Sagitta* may of course be coincidence, but this is at any rate the type of correlation worth watching for in future.

These few examples are sufficient evidence of the necessity for studying the movements of planktonic indicators, for it may be fairly said that they supplement the hydrographic observations. It is perhaps premature as yet to seek for further correlations until more detailed observations have been extended over a period of years. For future work it cannot be too strongly stressed that the distribution of the plankton-rich *S. elegans* water should be watched. The distribution and extent of this water will possibly be of considerable importance for the survival of the young of fish breeding in the area. It might perhaps, therefore, be expected that some such correlation will be shown for the haddock.

The year 1923 was an exceptionally good brood year for haddock and there is evidence that the plankton conditions were unusual in that year. The haddock fry appeared in unusual numbers in Danish waters where a good fishery resulted in the winter 1925—6. In 1923 the planktonic fauna in the Kattegat and Belt Sea was more oceanic than usual. The siphonophores *Physophora hydrostatica, Galeolaria truncata* and *Dimophyes arctica*, and euphausians were recorded. These conditions have been discussed by Kramp (1927, p. 183) who showed that a study of the Medusa fauna was of great assistance in understanding the relations and movements of the different water masses.

5) Fraser, J. H. The distribution of *Thaliacea* in Scottish waters, 1920—1938. Fisheries, Scotland, Sci. Invest. (unpublished).

The Practical Use of Indicators.

The more experienced the plankton worker, the wider is his knowledge of the species of the plankton as a whole. If he be a specialist in a large group such as the copepods he can recognize differences in the distribution of many species (see, e.g., Farran, 1920). In general, however, probably many of these species form the characteristic association of organisms which accompanies one or two more striking animals. It is these latter which should be selected as indicators, for it is essential for rapid examination of large numbers of collections that they should be easily seen.

The general association occurring with the few selected species should, however, be borne in mind, for under certain circumstances it may afford a valuable clue as to the type of water. It is possible, for instance, for the chosen indicator species to be itself absent. Thus pure *S. elegans* water may be recognized in some areas by the presence of large numbers of *Cosmetira, Laodicea, Aglantha, Themisto* and euphausians and the absence of indicators of other types of water, even though *S. elegans* itself be absent; for even the holoplanktonic species may show great seasonal fluctuations in their numbers.

Those species occurring in the plankton which have a bottom stage in their life history naturally show considerable seasonal fluctuations and are only of use as indicators in certain seasons. With a knowledge of the life histories and seasonal fluctuations in numbers of both holo- and mesoplanktonic animals a worker in one area will probably be able to see in his results much more than is at first obvious from the mere numerical data.

In regions of mixing it may not be so much the actual numbers of the indicators that are of importance, but rather the relative proportions of the indicators of the different types of water. The boundaries between waters of different types may sometimes be clearly defined by the plankton indicators. At other times there may appear to have been mixing over a considerable area. Unless collections have been made separately at different depths it will be necessary to examine the hydrographic data before any conclusions are attempted. A broad region of apparent mixing may be produced by water of one type overlying that of another type. An example may be found in the northern North Sea, where in the north-eastern area *S. elegans* and *S. setosa* may sometimes appear mixed. This has been shown by Fraser (1939) and Furnestin (1938) to be due to the presence of *S. elegans* water in the deeper layers.

A knowledge of the vertical distribution of the animals and of their habits of vertical migration must also be taken into consideration.

In practice it is probable that the larger plankton animals are more useful as indicators than unicellular organisms which reproduce very rapidly. An increased knowledge of the life histories and size changes of diatoms may, however, prove of value (see, e.g., Wimpenny, 1936, and Garstang, 1937).

In conclusion there are certain aspects connected with the use of plankton indicators to which future attention might profitably be directed.

The life histories of certain plankton animals have now been studied in detail and the differences in size of individuals of successive generations noted. To a certain extent it should thus be possible to follow the history of any one brood and its movements in the water masses from place to place. Such a study should be of great value in tracing the extent of the resultant water movement in a given time.

Some species also show structural variation according to geographical distribution and a detailed knowledge of these differences can be of value in tracing the origin of water masses. Possibilities in this direction have already been indicated by Fraser (1939) in a study of the varieties of *S. elegans.*

A close study should also be made of the mortality rates and reproductive capacities of different organisms as they are carried by water movements into areas in which their environmental conditions become changed.

All the above types of observation may prove of practical value, but they involve also problems of purely scientific interest, and if treated from the latter point of view they may in the end produce results of even greater practical importance. For bound up with the problems of variation, mortality, and reproduction is the question why certain organisms are apparently only able to survive in certain types of water.

One may postulate that in passing from the ocean to the coast changes in physical and chemical factors may gradually eliminate the purely oceanic species until a pure neritic community is reached. It is more difficult to suggest why this should act in the reverse direction, i.e., why neritic holoplanktonic organisms do not survive in pure ocean waters. These problems involve the study of the presence or absence of toxic or limiting substances, competition between species and their habits of life. Harvey's (1939) observation that the diatom *Ditylum* did not grow successfully in enriched natural sea water taken at certain times of year are significant. There are, however, many factors to be considered and it is beyond the scope of the present paper to discuss these.

It is at any rate certain that a study of the water from the biological viewpoint often throws quite a different light on observations made by more strictly hydrographical methods. In certain key localities also plankton indicators alone may prove of immense value as a guide to the general conditions. But the use of indicators should be regarded only as one more tool in the oceanographer's bag to help with other methods in picking the locks which bar us from knowledge of life in the sea.

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Intensity Fluctuations in Components of Solar Radiation with Atmospheric Conditions.

By

F. W. Ross and **C. L. Utterback,**

Physics and Oceanographic Laboratories, University of Washington, Seattle.

Introduction.

IN many types of observations of the effects of solar radiation it is desirable to know the intensity and variations in intensity of the total radiation as well as that of the different components. Such information is necessary, for example, in determining the absorption and scattering of daylight in natural water bodies where observations are made by taking submarine photometer readings at various depths. As the observations, at different depths, are not made at the same time, it is necessary to apply corrections for any variations of the intensity at the surface. Especially is this true of filters which admit only a narrow band of radiation when used in the photometer. Such corrections are determined by aid of a surface photometer which will measure the surface intensity at the same time as measurements are being made with the submerged photometer. As has been pointed out by Utterback and Jorgensen[1]), unequal variations of the intensity of different components of the surface light require a separate correction for each colour band which is used in the submerged photometer rather than for variations in its integrated response.

Daylight consists of light scattered by the atmosphere as well as direct sunlight. The relative intensities of these two constituents is a function of wave-length and depends upon the factors which control the scattering of light. Light is scattered at all angles from the scattering particles, and the intensity depends upon the angle of scattering, the wave-length of the light, and the size and number of molecules or particles in the path of the light beam. The size and number of particles present depends upon (1) atmospheric conditions such as temperature, pressure, humidity, and type of particles, (2) the

[1]) C. L. Utterback and Wilhelm Jorgensen. Journ. du Conseil, IX, 2, 197, 1934.

length of path through the atmosphere, which varies with time of day, time of year, and with latitude. The type of particles present, besides molecules, includes suspended materials which may be roughly described as dust, smoke, and clouds. Thus it is seen that there should be a variation in the wave-length-intensity distribution with change in weather conditions and with change in time of day.

The purpose of this investigation is to confirm these conclusions. No attempt has been made to analyse precisely the variation of wave-length-intensity distribution as a function of weather conditions but rather to indicate the necessity of correcting for each colour band separately. This has been done for relatively narrow bands of the visible spectrum by observing the relative intensities for those bands under various representative weather conditions and at different times of day. The observations were made at the Oceanographic Laboratories of the University of Washington located at Friday Harbor, Washington.

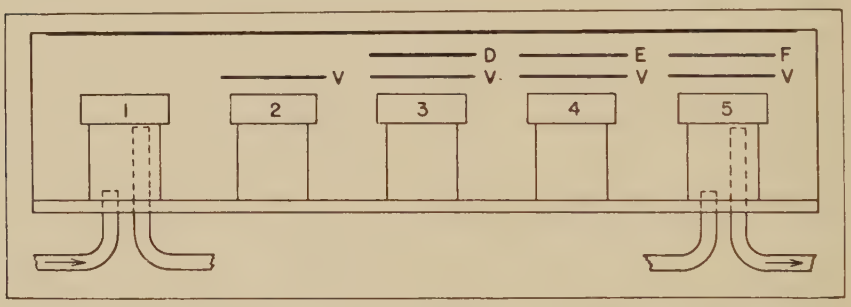

Fig. 1. A schematic diagram of the arrangement of the light-sensitive cells and the filters.

Five Photronic cells were arranged as shown in Fig. 1 and were placed at the top of a rigid twenty-foot pole in such a position that reflections from surrounding buildings had no effect. Since the temperature coefficient of these cells is appreciable, it was necessary to provide a means of keeping the cells at uniform temperature. This was done by replacing the composition back of the cell case with a water-cooled jacket. This jacket screwed into the case so that the entire sensitive surface was held at about one millimetre from a metal plate which was maintained at a uniform temperature by means of a constant water flow. The water jacket also served as a mounting for the cell.

The cells were all provided with a diffusing screen and with filters as follows:— Cell 1, whose sensitivity curve is shown at A, Fig. 2, had no filters and Cell 2 was provided with a filter, V, which gave the cell a resultant sensitivity curve shown at B, Fig. 2. It may be observed that the sensitivity curve for Cell 2 is approximately the same as that for the average eye, which is shown for comparison at C, Fig. 2.

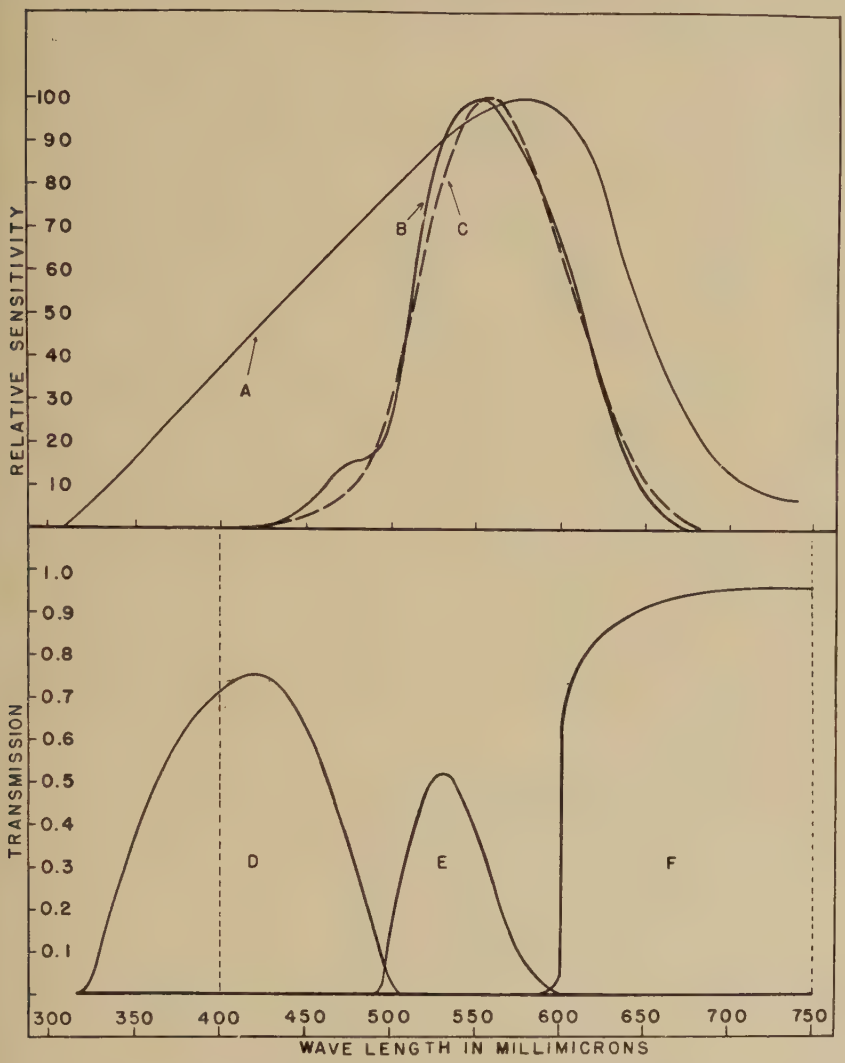

Fig. 2. Transmission characteristics of the filters and the spectral response curves of the cells. The sensitivity curve of the eye is included for comparison.

In addition to the diffusing screen and filter V, Cells, 3, 4, and 5 were provided with a colour filter, the transmission characteristics of which are shown by curves D, E, and F, Fig. 2. By employing these filters the visible wave-length region is divided into three bands with no appreciable overlapping.

Under the conditions of the experiment the current-illumination characteristics of the cells are approximately linear; therefore, since absolute intensities are not needed, only relative current values have been given.

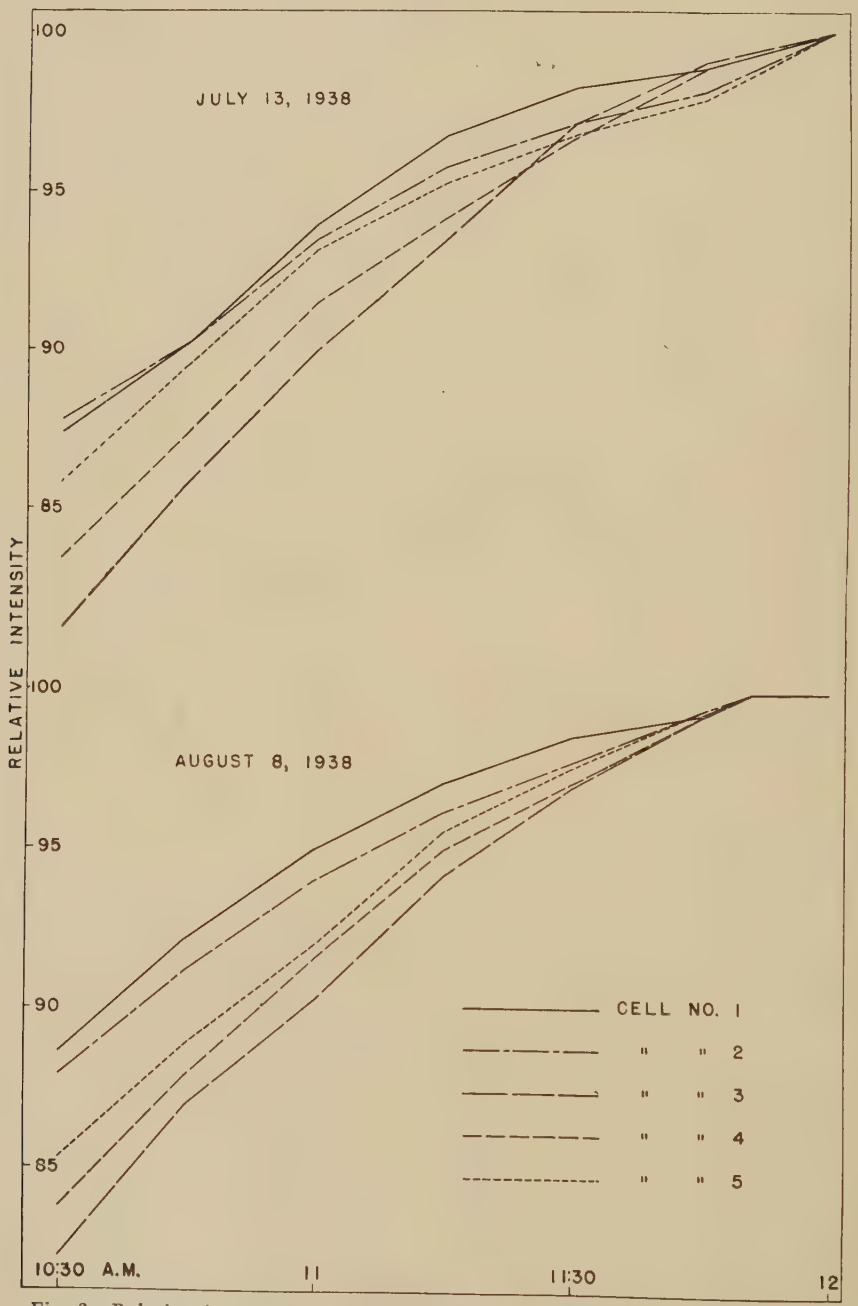

Fig. 3. Relative intensities, on two clear days, as recorded by the five cells, expressed in percentages of the intensity at twelve o'clock noon.

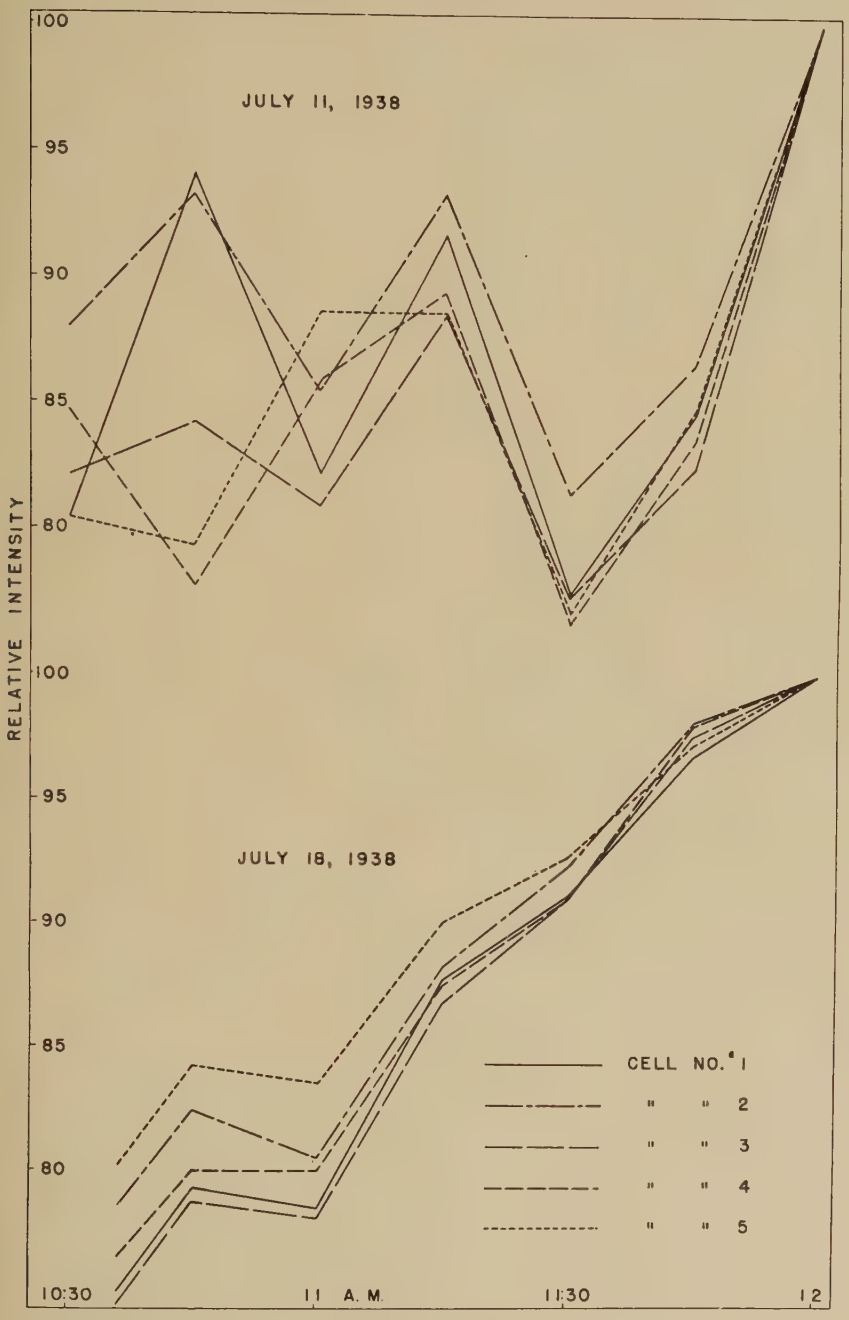

Fig. 4. Relative intensities, on a cloudy day (upper curves), and on a hazy day, as recorded by the five cells, expressed in percentages of the intensity at twelve o'clock noon.

Procedure.

The current from each of the five cells was read successively by means of a switching arrangement with a single micro-ammeter. This operation required about one minute. If any variation occurred during this time another set of observations were taken the following minute. This check was only necessary during unsettled weather conditions. Readings which could not be duplicated in this manner were discarded. In this way observations were made at intervals which varied from 5 to 15 minutes on a number of days representing characteristic types of weather conditions. The observations were made from about 10 a.m. to 2 p.m.

Data.

Weather conditions have been classified as (1) clear, (2) cloudy, and (3) hazy.

On a number of days forest fires prevailing on Vancouver Island, which lies to the west and north of Friday Harbor, caused a general overcast of smoke which has been referred to as haze. For conditions where the sky is overcast with a small amount of such smoke as well as a thin layer of clouds this classification is arbitrary, and depending upon the amount of clouds and haze present, falls into one or another of the classes. Observations were made throughout the summer of 1938. From these observations certain days were selected which were characteristic of the three types.

In Table 1 are found data taken during the forenoon of one day characteristic of each type. As the data for the afternoon are similar to those for the forenoon they have not been included. While observations were made very frequently, it was not possible for each one to fall exactly on the quarter hour. A few of the values given in Table 1 are interpolations between close actual observations. In order to compare the intensity variation for days not having the same actual intensity the observations have been reduced to percentages of the twelve o'clock value for that day. The graphs of the variations in these percentages during the forenoon of the three characteristic days are shown in Figures 3 and 4.

Inspection of the graphs shows that the variation of intensity for the various wave-length bands used was not the same under different weather conditions. On July 13th, a clear day, there is a variation of 18·8 per cent. from 10·30 a.m. to 12·00 noon in the intensities for Cell 3. Corresponding to this was the variation of 16·6, 14·2, 12·6, and 12·2 per cent. for Cells 4, 5, 1, and 2 respectively. On July 18th, a hazy day, the variations from 10·36 a.m. to 12·00 noon were 25·4, 24·9, 23·5, 21·5, and 19·8 per cent. for Cells 3, 1, 4, 2, and 5 respectively. Not only is this variation larger than for the clear day but in addition the order of variation is changed. The variation for Cell 1 was next to the least on the clear day, while on the hazy day it was

Table 1.

Relative Intensities on four Characteristic Days.

Time	Relative Intensity				
	Cell No. 1	Cell No. 2	Cell No. 3	Cell No. 4	Cell No. 5
			July 13th.		
10·30	15·9	18·8	38·2	23·1	16·3
10·45	16·4	19·3	40·4	24·2	17·0
11·00	17·1	20·0	42·4	25·3	17·7
11·15	17·6	20·5	44·0	26·1	18·1
11·30	17·9	20·8	45·8	26·8	18·4
11·45	18·0	21·0	46·7	27·4	18·6
12·00	18·2	21·4	47·1	27·7	19·0
			August 8th.		
10·30	12·4	15·9	32·3	20·1	13·8
10·45	12·9	16·5	34·2	21·1	14·4
11·00	13·3	17·0	35·5	22·0	14·9
11·15	13·6	17·4	37·0	22·8	15·5
11·30	13·8	17·7	38·1	23·3	15·8
11·45	13·9	18·0	39·0	23·8	16·1
12·00	14·0	18·1	39·3	24·0	16·2
			July 11th.		
10·30	13·5	17·0	38·0	22·0	14·7
10·45	15·8	18·0	39·0	20·2	14·5
11·00	13·8	16·5	37·5	22·3	16·2
11·15	15·4	18·0	41·0	23·2	16·2
11·30	13·0	15·7	35·8	19·8	14·0
11·45	14·2	16·7	38·2	21·7	15·5
12·00	16·8	19·3	46·3	26·0	18·3
			July 18th.		
10·30	8·8	11·7	23·0	15·0	11·8
10·45	9·8	12·6	25·0	16·0	12·7
11·00	9·6	12·3	24·8	16·0	12·6
11·15	10·8	13·5	27·6	17·5	13·6
11·30	11·2	14·1	28·9	18·2	14·0
11·45	11·9	15·0	31·0	19·6	14·7
12·00	12·3	15·3	31·8	20·0	15·1

next to the greatest. Variations for Cells 5, 4, and 3, however, maintain the same order on both days.

The changes occurring on the cloudy day are considerable even during a fifteen-minute period. For example, from 10·45 to 11·00 a.m. not only did the order of percentage variation for Cells 5, 4, and 3 change but Cells 5 and 4 increased from 79·3 to 88·6 per cent. and 77·7 to 85·9 per cent. respectively while Cells 2, 1, and 3 decreased from 93·3 to 85·5, 94·1 to 82·2, and 84·2 to 80·9 per cent. respectively.

These changes in intensity were caused by variation in the angle of the sun and by variations in the distribution of clouds, water vapour, and smoke. On days classified as of a given type the manner of

variation is similar to that of the days shown in Figures 3 and 4. For weather conditions which cannot be classified in intensity definitely as of a given type, the variations in intensity were not exactly as shown here but were intermediate between the intensity variations of two types. Thus on August 8th the weather was clear but the relative humidity was higher than on July 13th. From the data as shown in Table 1 and the curves in Figure 3 it is seen that the variation is nearly the same as for July 13th in the case of Cell 1. (In outdoor photography these results are of some importance particularly when using filters and photo-electric exposure meters.)

In view of the data presented here it is seen that no accurate prediction of the variation in intensity of one wave-length band can be made from the variation of another, or from the variation of the integrated response of a cell of the type used.

Die Bestimmung des Chlorophylls in Meerwasser-Schöpfproben.

Von

Johannes Krey,

Institut für Meereskunde der Universität Kiel.[1])

BEI produktionsbiologischen Untersuchungen erfasst man die produzierte Menge meist durch Auszählung der Zellen bzw. der Individuen, durch das Absetzvolumen, durch die Bestimmung des Gewichts oder des gebundenen Phosphors. Die Zellzählungen ergeben zwar mit den modernen Methoden eine genaue Bestimmung der Zahl der Zellen, jedoch nur der *Zahl.* Über Grösse, Masse, Assimilationsfähigkeit usw. können diese Zahlen wegen der verschiedenen Zellgrösse, Zellformen und des verschiedenen Chlorophyllgehaltes — selbst innerhalb derselben Species — nur eine ganz rohe Vorstellung geben. Ja, es erscheint häufig unsinnig, wenn man die Masse der Gesamtphytoplanktonproduktion durch die Summe der verschiedensten Species, die sich in Grösse und Masse um das Vieltausendfache unterscheiden können, ausdrücken will. Harvey hat zum ersten Mal versucht, für die Bestimmung der produzierten Menge ein physiologisches Mass zu finden in der Menge des im Phytoplankton vorhandenen Chlorophylls. Dieses Chlorophyll gibt ein Mass für die Produktionskraft in einem bestimmten Wasservolumen. Auf der Grundlage von Assimilationsversuchen ergibt dann das Chlorophyll zusammen mit den die Assimilation auslösenden bzw. beeinflussenden Faktoren wie Licht, Temperatur, Salzgehalt und Nährstoffgehalt ein Mass für die in der Zeiteinheit produzierte Stoffmasse.

Wohl fehlt es nicht an genauen Methoden zur Bestimmung der zuletzt genannten Faktoren. Die bislang ausgeführten Chlorophyllbestimmungsmethoden arbeiteten jedoch mit grösseren Wassermassen oder mit Netzfängen. Von einer den Methoden zur Bestimmung des Salzgehalts, der Temperatur und der Nährstoffe gleichwertigen Chlorophyllbestimmung muss man jedoch verlangen, 1) dass die zu untersuchende Probe punktförmig genommen werden kann; 2) dass sämtliches Chlorophyll erfasst wird (also auch das im Nannoplankton enthaltene); 3) dass die Proben ähnlich den vorgenannten Bestimmungen serienmässig genommen und verarbeitet werden können.

[1]) Meereskundliche Arbeiten der Universität Kiel Nr. 65.

Es ist bereits eine Reihe von Chlorophylluntersuchungen im Meerwasser vorgenommen worden. Sie alle beruhen letzten Endes auf der Möglichkeit, aus der Farbintensität des in einem geeigneten Lösungsmittel gelösten Chlorophylls dessen Gewichtsmenge zu berechnen. Die Art und Weise, das Chlorophyll aus der sehr verdünnten Suspension, die das Phytoplankton im Meere bildet, in das Lösungsmittel zu überführen, ist recht verschieden. An dieser Stelle liegen die grössten Schwierigkeiten, besonders, wenn man mit kleinen Mengen Wasser eine zur Messung genügende Farbintensität erhalten will.

Die meisten bisherigen Verfasser arbeiten mit Netzfängen (vgl. Kreps und Verjbinskaya 1930, Harvey 1934, Gilson 1937, Gillam, Ridi und Wimpenny 1939). Sie verzichten dabei auf eine Erfassung des Nannoplanktons sowie auf eine punktförmige Probennahme. Ausserdem ist in manchen Fällen die Menge des durch das Netz filtrierten Wassers nicht genau bekannt. Nur einige limnologisch arbeitende Autoren haben auch das Nannoplankton mit in die Chlorophyllbestimmung eingeschlossen, so Riley 1938, der 1 Liter Wasser durch ein Whatman-Filter filtrierte und Kozminski 1938, der aus 5—15 Liter mit einer Superzentrifuge das gesamte Plankton isolierte.

Die Messung der gewonnenen Extrakte geschieht entweder kolorimetrisch durch Vergleich gegen die Harvey-Standardlösung (vgl. Harvey, Riley, Gilson) oder photometrisch bzw. spectrophotometrisch im Gebiet des ersten Absorptionsmaximums des Chlorophylls bei 666 mμ (Kozminski, Gillam, Ridi und Wimpenny). Bei der kolorimetrischen Bestimmung tritt aber immer wieder die Schwierigkeit auf, dass die Chlorophyllproben durch wechselnden Gehalt an braunfärbenden Stoffen u.U. schwer mit dem Standard zu vergleichen sind.

Nur Kozminski hat durch Verwendung der Zentrifuge und des Photometers bzw. Spectrophotometers die Schwierigkeiten in der Materialbeschaffung und dessen Messung umgangen. Da er jedoch mit grösseren Wassermengen (5—15 Liter) arbeitet und nicht überall eine Superzentrifuge zur Verfügung steht, musste hier nach einer Vereinfachung gesucht werden.

Um die Nachteile, die durch die Verwendung der Netzfänge und des Kolorimeters gegeben sind, zu umgehen, sowie die eingangs gestellten Forderungen der punktförmigen Probennahme, der restlosen Erfassung aller chlorophyllhaltigen Phytoplanktonten und der serienmässigen Aufarbeitung zu erfüllen, habe ich auf Anregung von Prof. Wattenberg versucht, ein anderes Verfahren zu entwickeln. Dieses ist durch folgende Merkmale charakterisiert: 1) die Verwendung so geringer Wassermengen, wie sie im normalen Wasserschöpfer zur Verfügung stehen. 2) Die Filtration durch Ultrafilter, durch die das gesamte Phytoplankton zurückgehalten wird. 3) Die photometrische Bestimmung des Chlorophylls und seine optische Trennung von den Carotinoiden.

Die Probennahme vollzieht sich etwa folgendermassen: es werden

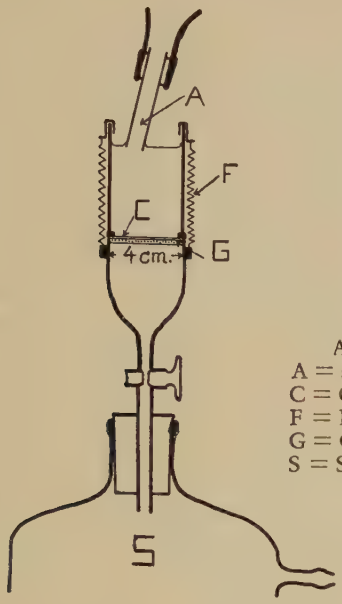

Abbildung 1: Stefi-Filter-Apparatur.
A = automatischer Flaschenauslauf.
C = Cella-Filter von 4 cm. Durchmesser.
F = Feder zum Halten des Filteraufsatzes.
G = Glasfilterplatte.
S = Saugflasche.

1 l.-Flaschen abgefüllt und entweder gleich an Bord filtriert, sofern dieses irgend möglich ist, oder innerhalb kürzester Frist an Land verarbeitet. Die Filtration erfolgt bei Unterdruck durch ein Cella-Filter von 4 cm. Durchmesser mit einer maximalen Porenweite von 1 μ. Es wird dabei die verhältnismässig kleine Stefi-Filter-Apparatur (Stefi 4, von der Firma Membranfilter-Gesellschaft Göttingen) benutzt (vgl. Abb. 1).

Die Filtrationszeit beträgt je nach dem vorhandenen Plankton und der Menge der im Wasser vorhandenen Kolloide ¼ Stunde und mehr. Das Filter wird mit dem darauf haftenden Niederschlag kurz (etwa ¼ Min.) über Wasserdampf erhitzt. Damit soll erreicht werden, dass die Chlorophyllase, die in alkoholischer Lösung den Ersatz der Phytylgruppe des Chlorophylls durch Methyl hervorruft, zerstört wird. Darauf wird das Filter in einer 50 ccm.-Weithalsflasche mit 6—8 ccm. reinem Methylalkohol übergossen. Dadurch werden die Pflanzenfarbstoffe extrahiert. Die so behandelten Filter können in den sorgfältig verschlossenen und dunkel gehaltenen Flaschen ohne wesentliche Änderung der Farbstoffkonzentration aufbewahrt werden.

Vor der Darstellung der weiteren Bearbeitung müssen wir noch kurz einige Voraussetzungen bringen. Eine Analyse von Diatomeenfarbstoffen, wie sie mehrfach unternommen worden ist (vgl. Kylin 1927, Montfort [noch unveröffentlicht]), fördert eine ganze Anzahl von verschiedenen Komponenten zutage. Hauptsächlich sind vertreten Chlorophyll *a*, Xanthophyll, Fucoxanthin, Carotin und Phylloxanthin. Dieselben Stoffe finden wir mit einigen Abweichungen auch bei den Cyanophyceen, Dinoflagellaten und Braunalgen. Sie

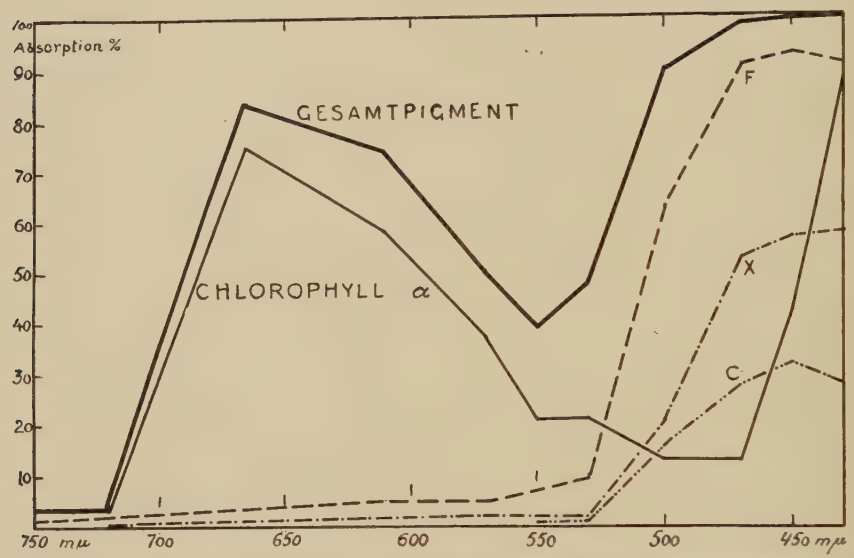

Abbildung 2: Absorptionskurven von Diatomeenfarbstoffen (chromatographische Analyse von C. Montfort).
F = Fucoxanthin. X = Xanthophyll. C = Carotin.

enthalten alle verschwindend wenig Chlorophyll *b*. Dagegen findet sich in den Chlorophyceen viel Chlorophyll *b*. Chlorophyll *a* unterscheidet sich von Chlorophyll *b* optisch durch eine andere Lage der Absorptionsmaxima. Diese Tatsache ist für die photometrische Bestimmung von Bedeutung. Beide Chlorophylle zeigen zwei Absorptionsmaxima. Für Chlorophyll *a* liegen diese bei 666 mμ und bei 430 mμ (vergl. Fig. 2). Wenn wir also Chlorophyll *a* photometrisch bzw. spectrophotometrisch bestimmen wollen, müssen wir bei einem dieser beiden Maxima die Absorption bestimmen. Wir können fernerhin auf Grund von Bestimmungen von Montfort das Verhältnis der Absorptionen bei 430 und 666 mμ zu 1·8 bis 1·9 ansetzen. Damit können wir aus dem Wert des einen Absorptionsmaximums den des anderen berechnen.

Dagegen zeigen die Carotinoide nur ein Hauptmaximum im sichtbaren Spectralbereich, und zwar im kurzwelligen Gebiet (vgl. Fig. 2). Man wird ihre photometrische oder spectrophotometrische Bestimmung also im kurzwelligen Bereich vornehmen.

Die Abb. 2 zeigt den Verlauf der Absorption der Farbstoffkomponenten von Diatomeen. Dieser Abbildung liegen Analysen von Montfort zugrunde von Diatomeenmaterial aus einem Brackwasser bei Halle. Die Absorptionswerte der Carotinoide im langwelligen Bereich wurden ergänzt nach früheren Untersuchungen Montforts an Phäophyceen, die in Bezug auf die Assimilationsphysiologie den Diatomeen sehr nahe stehen. Da nach Montfort die Carotinoide für die Assimilation zumindest der Tiefenphäophyceen eine erhebliche Rolle spielen, messen wir auch den Gehalt des Phytoplanktons an

Carotinoiden, d.h. an braunen Farbstoffen. Dabei bleibt noch die Frage offen, ob es sich bei diesen braunen Farbstoffen, die wir aus dem Filtersatz ausziehen, um intakte, funktionsfähige Carotinoide handelt oder um braune Detritusfarbstoffe. Dieses muss durch weitere Untersuchungen geklärt werden.

Aus dem Verlauf der Absorptionskurven der verschiedenen Diatomeenfarbstoffe ziehen wir die Folgerung, dass die Bestimmung des Chlorophylls bei 666 mμ und die der Carotinoide bei 430 mμ vorzunehmen ist. Bei der Berechnung ist folgendes zu beachten. Der Chlorophyllwert kann wegen der Geringfügigkeit der Carotinoidabsorption bei 666 mμ praktisch direkt bestimmt werden. Dagegen wird der Carotinoidwert berechnet durch Subtraktion des entsprechenden Chlorophyllwertes von der Gesamtabsorption bei 430 mμ. Wenn wir also bei 666 mμ eine Extinktion a haben, dann beträgt die Chlorophyll-Extinktion bei 430 mμ $1{\cdot}8 \cdot a$. Die Gesamtextinktion bei 430 mμ betrage b. Dann ist der Carotinoidwert gleich $b - 1{\cdot}8 \cdot a$.

Die Messung der in der vorher dargestellten Weise gewonnenen Planktonextrakte geschieht folgendermassen: Der durch ein kleines Papierfilter filtrierte methylalkoholische Extrakt wird auf ein Gesamtvolumen von 10 ccm. gebracht. Dieses Volumen reicht aus zum Vorspülen und Füllen einer Microküvette von 150 mm. Schichtdicke. Mit dem Zeiss'schen Pulfrich-Photometer wird die Durchlässigkeit für die Wellenlängen 666 und 430 mμ gemessen.

Dabei ist jedoch folgendes zu beachten. Das Filter S66·6 (666 mμ) zeigt eine für diese Messungen reichlich grosse Filterbreite. Da in diesem Filterbereich eine Absorptionskante des Chlorophylls liegt, sind die Extinktionen verschiedener Schichtdicken einander nicht genau proportional. Diese Abweichungen sind nun zwar bei dem benachbarten Filter S63 (630 mμ) nur unbedeutend. Jedoch ist die Absorption des Chlorophylls in diesem Gebiet nur etwa ½ bis ⅔ so gross als bei S66·6. Wir haben also zugunsten der grösseren Empfindlichkeit am Filter S66·6 festgehalten und für die verschiedenen Schichtdicken bzw. Extinktionen eine Korrektionskurve aufgestellt (vgl. Abb. 3). Dabei haben wir die Extinktion einer Lösung von 1 mg. Chlorophyll *a*[1]) in 100 ccm. Methylalkohol bei einer Schichtdicke von 1 cm. von $E = 284$ als Grundwert angenommen. Alle höheren Extinktionen müssen danach mit einem Korrektionsfaktor, der grösser ist als 1, und alle niedrigeren mit einem, der kleiner ist als 1 versehen werden.

Der von Filter S43 (430 mμ) durchgelassene Strahlenbereich wird vom Auge schlecht aufgenommen. Es ergeben sich somit Ablesungsfehler, die grösser als bei Filter S66·6 sind. Das Filter S45 (450 mμ) zeigt wiederum den Nachteil einer zu grossen Filterbreite und damit bei diesen Lösungen eine Farbdifferenz.

Über die *Empfindlichkeit* der Methode ist folgendes zu sagen. Unter der Voraussetzung, dass man bei Filter S66·6 eine Extinktion von 43 noch ohne grossen Fehler ablesen kann, würde man bei einer Schichtdicke von 15 cm. noch eine Konzentration von 10 γ/100 ccm., d.i.

[1]) Chlorophyll *a*, chromatographisch rein, von der Firma Sandoz, Basel.

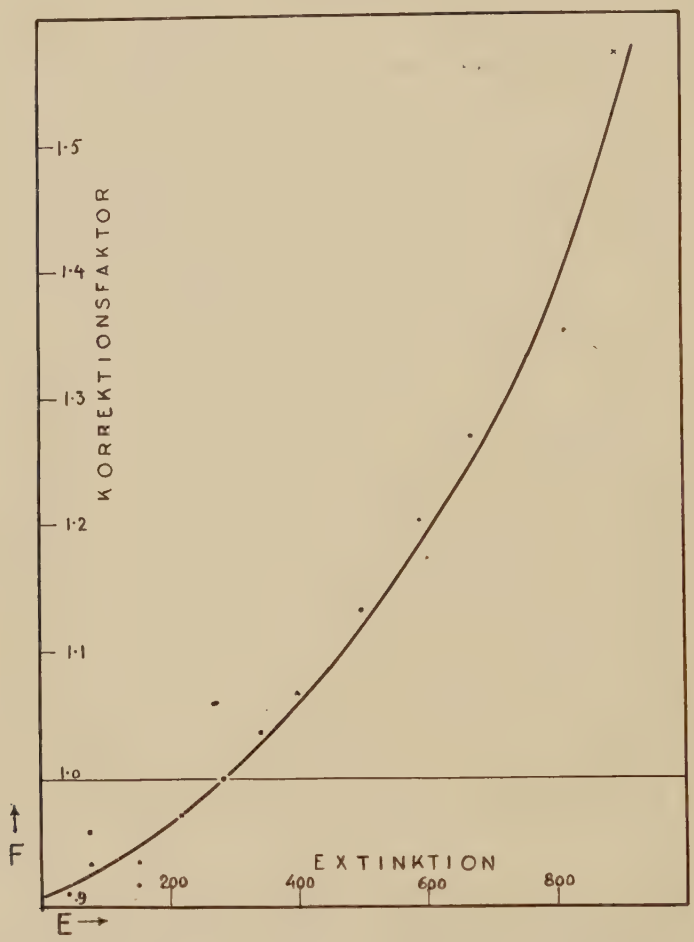

Abbildung 3: Korrektionskurve für die bei 666 mμ (Filter S 66·6 des Zeiss'schen Pulfrichphotometers) gemessenen Extinktionen für Chlorophyll a.

1 γ/10 ccm. messen können. Da das Plankton von 1 Liter auf 10 ccm. konzentriert wird, kann man also noch 1 γ Chlorophyll *a* in 1 Liter Seewasser nachweisen. Vergleichsweise sei noch eine Chlorophyllbestimmung an einer Reinkultur von *Chaetoceras gracile* gegeben. Dabei ergab sich:

$4{\cdot}3 \cdot 10^5$ Zellen = 66 Extinktions-Einheiten
und da 1 γ/10 ccm. = 43 „ „
so ist $4{\cdot}3 \cdot 10^5$ Zellen = 1·5 γ Chlorophyll a

1 Zelle hat ein Volumen von 30 μ^3. Somit ergibt sich, dass ein Zellvolumen von 1 mm^3. *Chaetoceras gracile* einen Chlorophyllgehalt von 116 γ hat.

Um die *Genauigkeit* des Verfahrens zu prüfen, wurde an einer

Stelle der Kieler Aussenförde eine grössere Menge Oberflächenwasser genommen. Hieraus wurden 9 Proben genommen und deren Chlorophyllgehalt untersucht. Beifolgende Tabelle zeigt das Untersuchungsergebnis.

Nr. Probe	Wassermenge ccm.	[1])Ek 666 für 1 l.	Abweichung vom Mittelwert (E)	
1	1000	194	— 2	
2	1000	194	— 2	
3	1000	190	— 4	Mittlere
4	1000	202	+ 6	Abweichung
5	1000	202	+ 6	= 10·6
6	1000	232	+ 36	= 0·24 γ
7	550	189	— 7	= 5·4 %
8	500	172	— 24	
9	400	188	— 8	

Mittelwert 196 = 4·5 γ/l.

[1]) Anm.: Hierin bedeuten: E die Extinktion, Ek die mit der optischen Korrektur versehene Extinktion.

Die Empfindlichkeit der hier geschilderten Methode kann noch gesteigert werden, wenn man 1) grössere Wasservolumina verwendet und 2) grössere Schichtdicken benutzt bei gleichbleibendem Volumen der Küvetten. So würden sich z.B. Küvetten von 250 mm. Schichtdicke und 10 ccm. Volumen herstellen lassen.

Zum Schluss sei noch als Beispiel für die Anwendungsmöglichkeit dieser Methode eine Untersuchung des Wassers auf einer Station in der nördlichen Kieler Bucht im März 1939 gegeben (Abb. 4). Das Diagramm zeigt uns zunächst eine Salzgehaltsschichtung mit einer Sprungschicht bei 20 m. Diese Schichtung spiegelt sich auch wider in der Verteilung von P und N: wir finden in der Oberschicht eine Armut an diesen Nährstoffen, in der Unterschicht einen grösseren Reichtum. Die Chlorophyllkurve zeigt mehrere Besonderheiten: 1) Wir finden in der Oberschicht ein Chlorophyllmaximum in 5 m. Die Erscheinung, dass dieses Maximum nicht in 0 m. liegt, fanden bereits andere Autoren (vgl. Kozminski u.a.). 2) Es findet sich eine ausserordentlich starke Anreicherung in der Sprungschicht. Sie dürfte auf abgesunkenes Plankton zurückzuführen sein. 3) Ein gleicher Grund wäre für die relative Anreicherung dicht über dem Boden verantwortlich zu machen.

In einer späteren Untersuchung wird auf diese Erscheinungen sowie auf die Verteilung der Carotinoide einzugehen sein.

Zusammenfassung.

In der vorliegenden Arbeit wird eine Methode angegeben zur Chlorophyllbestimmung, die drei Forderungen erfüllt. 1) Sie gestattet durch Verwendung geringer Wassermengen eine punktförmige Probenahme. 2) Es werden durch Verwendung von Ultrafiltern sämtliche chlorophylltragende Phytoplanktonten erfasst. 3) Die zur Untersuchung

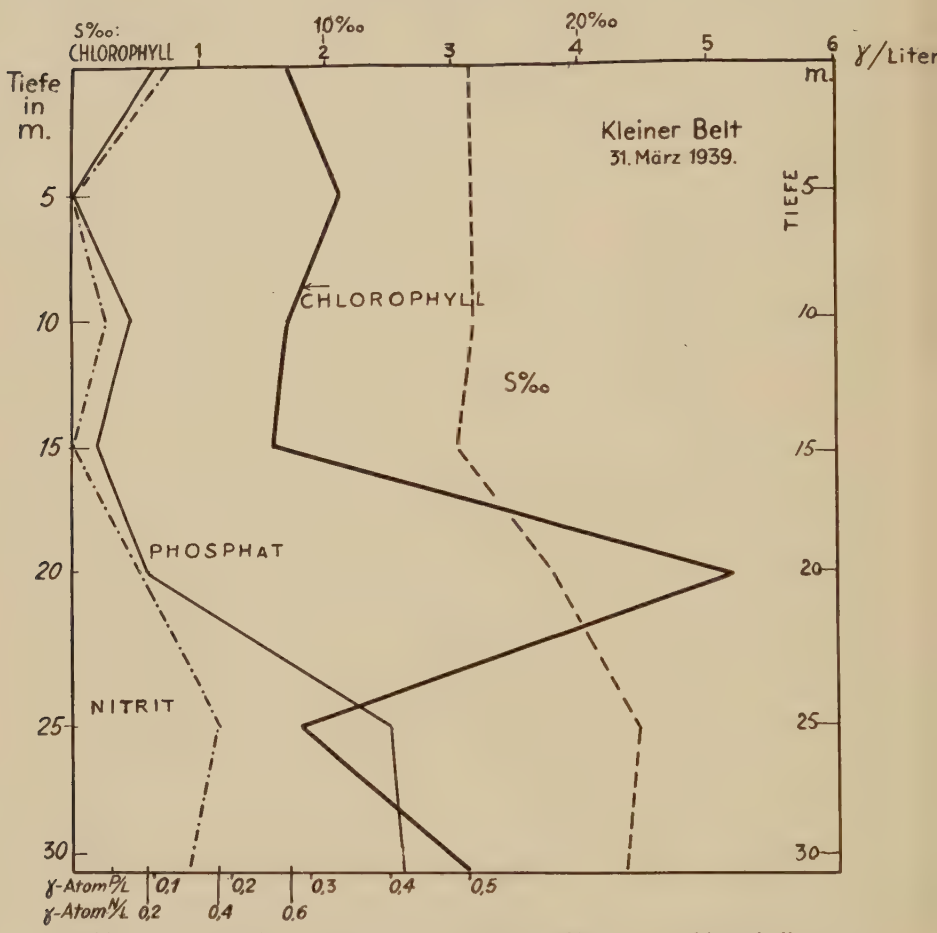

Abbildung 4: Vertikale Verteilung von Salzgehalt (S‰) ----, Chlorophyll ———, Phosphat ——— und Nitrit ·-·-· im Kleinen Belt am 31.III.1939.

gelangenden Proben können serienmässig genommen und verarbeitet werden. In dem beschriebenen Arbeitsgang werden ausser dem Chlorophyll auch die braunen Planktonpigmente — meist Algencarotinoide — bestimmt. Mit dieser Methode kann noch 1 γ Chlorophyll/l. bestimmt werden. Bei einem Gehalt von 4·5 γ/l. ergab sich ein mittlerer Fehler von 5·4 %.

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The Control of Diatom Populations by Grazing.*)

By

Richard H. Fleming,

Scripps Institution of Oceanography,
University of California, La Jolla, California.

MARINE plankton diatoms are the great primary food producers of the sea. However, their distribution is far from uniform and in areas where dense populations may be found there are usually tremendous seasonal variations in their numbers. Areas where dense populations occur are usually in high latitudes or near shore where winter mixing or upwelling occur. One of the major problems of oceanography has been the study of the regional and time variations of diatom populations and the environmental conditions which cause them. In such investigations, the species of diatoms present have been studied and great emphasis has been placed on the importance of certain physical factors, such as light intensity, temperature, and stability, and on variable chemical constituents of the water, principally the so-called plant nutrients, that is, inorganic compounds of nitrogen, phosphorus, silicon, iron, etc. This discussion will deal specifically with the effect of grazing on the time variations in diatom populations.

For the purpose of the discussion it is assumed that the physical and chemical factors of the environment are such that the division rate of the diatoms remains constant. This implies an abundant supply of the essential plant nutrients, suitable physical conditions, and sufficient light. The discussion is concerned with the time changes in the population of a given water mass, and the conclusions cannot be applied to time variations at any point or in any region unless it is established that the advective changes due to differences along the lines of flow are negligible. Two other assumptions are essential to the discussion; first, that there is a "seed" stock of diatoms which can develop under the prevailing conditions and that there are zooplankton forms which will feed or graze upon the species of diatoms present,

*) Contribution from the Scripps Institution of Oceanography. New Series, Number 65.

and second, that the fraction of the population removed each day by grazing is variable. In order to emphasize the importance of grazing in determining the variations in the diatom population let us consider the following points:—

1. What are the conditions necessary for the development of large diatom populations? Obviously the physico-chemical environment must be optimal, or nearly so, for the species present. Furthermore, grazing, or the removal of diatoms, must be less than the rate at which they are being produced.

2. What factors determine the maximum populations which occur from time to time? It has been suggested that the reduction of one or more of the essential elements below a threshold level may limit the population. However, this cannot apply as the nutrients continue to fall *after* the time of maximum population, (for example, Harvey, Cooper, Lebour and Russell, 1935—36).[1]) It will be shown later that the maximum population may be determined by the rate of division and the rate at which the population is being consumed by grazers.

3. What conditions bring about a decrease in the diatom population? Obviously during a period when the population is decreasing the rate of production must be less than the rate of removal. Diatoms may disappear from the photosynthetic zone only by sinking, death and decomposition, or by grazing. Harvey *et al.* consider that sinking is an extremely slow process and imply that diatoms rarely, if ever, die a "natural death". Hence it follows that grazing must be the main factor which will reduce the diatom population.

4. What factors determine the time of year at which maximum populations occur? It would appear reasonable to assume that maximum populations will occur when the physico-chemical environment is favourable so that the diatoms will be dividing actively. Maximum populations are usually found during the spring and summer months, so we may assume that during these seasons the conditions are optimal for diatom growth. It will be shown later that the appearance of one or more peaks in the diatom population during the course of the year may be largely determined by fluctuations in the amount of grazing.

Population and Production.

Before proceeding it is advisable to have a clear understanding of the terms population and production. Population is a measure of the number of individuals in a given volume. In the ocean we are usually dealing with mixed populations containing a variety of species which may have widely differing sizes. Even when there is only a single

[1]) Hereafter this paper will be referred to as Harvey *et al.*

species, there may be a considerable range in the size of individuals. When dealing with diatoms as food producers we are not concerned with individuals but rather with the ability of the total population to fix carbon, nitrogen, phosphorus, etc., in a form available to animals. Unless we have knowledge of the relative sizes of the different species of diatoms, an enumeration of the numbers of different species of diatoms in a given volume is of little help in determining the food value of the population. Volumes of the phytoplankton in a given volume, determined by settling or centrifuging, have been used by various workers, but this method is not desirable because of the widely variable shapes and effective volumes of the different types of cells. Weighing is also unsatisfactory, on account of the great range in the relative weight of the silicious tests in different species. Chemical methods, such as the determination of carbon, nitrogen, or phosphorus, in phytoplankton samples give a good measure of the food value of the population, but such analyses are difficult and time-consuming, and unsuitable for general use. Furthermore, there is the difficulty of separating the diatoms from the zooplankton organisms. The most suitable unit of reporting diatom populations, where the investigation is not concerned with the biology of the different species, appears to be that developed by Harvey (1934) for determining the pigment content of the plankton catch and reporting this in plant pigment units. Another method developed by Harvey *et al.* which lends itself to this problem is that of reporting the diatom population in terms of diatoms of "average cell contents". This method requires a knowledge of the cell contents of the different species dealt with, and as these are variable, would require considerable care in the handling of the data. However, in dealing with the large diatom populations which occur in the ocean, it is generally true that they are predominantly composed of only one, or a few, species. In these cases, enumeration gives at least relative values of the food value of the population. Of course, any study of the population is based on sampling methods which are themselves usually subject to large errors.

It has been pointed out that the diatom population can be represented by enumeration, in terms of plant pigment units, average cells, etc., per unit volume. The production, that is, the number of units, (enumeration, plant pigment units, or average cells) formed per unit volume in unit interval of time can therefore be reported in comparable units. In the following discussion the expression *production* will be used to express the time-rate of formation of additional units due to growth and division. If the production is integrated over a given time interval, we obtain the *total production* for that interval. This is the total number of units formed from the original population. When the diatom population is subject to grazing, many of the units produced are consumed. The *increment* in population will designate the difference between the initial population and the population at some later time. Only in the absence of grazing, or removal by other means, will the total production be the same as the increment in

population. Where the removal is by grazing only, the difference between the total production and the population increment in a given time interval will be referred to as the *yield*. In the following discussion the expression "cells" will be used, but this may be interpreted as any suitable unit for reporting population or production.

Basic Equation and Definition of Terms.

Thus far the changes in the diatom population and the grazing by zooplankton have been discussed in very general terms. In order to set up an equation we must limit the conditions. We shall deal with the situation where the diatom population is initially rather small, increases, passes through a maximum, and then decreases. It will be assumed that there is a certain amount of grazing at the start and that this increases at a constant rate. The "grazing" in this case does not refer to absolute number of units of the diatom population but to the fraction of the population removed in a given interval. Throughout the following discussion the unit of time considered is a day.

On the above assumptions we may set up the following equation:—

$$\frac{dP}{dt} = P\,[a-(b+ct)] \tag{1}$$

where $\frac{dP}{dt}$ is the time rate of change of the diatom population, P is the population, a is an expression for the rate of division, b is an expression for the initial grazing rate, and c the rate at which the grazing increases. The constants, a, b and c, are all taken as positive. It may seem directly from this equation that if the population, P, is at a maximum, that is, $\frac{dP}{dt} = 0$, then,

$$a = b+cT \tag{2}$$

where T is the time interval between the initial and maximum populations. At the time T, the rate of increase is just balanced by the removal by grazing.

If equation (1) is integrated we obtain,

$$P_t = P_0 e^{(a-b)t-\frac{1}{2}ct^2} \tag{3}$$

or,

$$\ln \frac{P_t}{P_0} = (a-b)t - \frac{1}{2}ct^2 \tag{4}$$

where P_0 is the initial population. From this equation the population curve can be plotted for the interval $t = 0$ to $t = 2T$. This curve is bell-shaped and symmetrical (see Fig. 1).

The *diurnal multiplication index, a,* is considered as constant and is independent of grazing. The *diurnal multiplication factor* which determines the value of a can be expressed as follows:—

$$\frac{P'_{t+1}}{P_t} = e^a \tag{5}$$

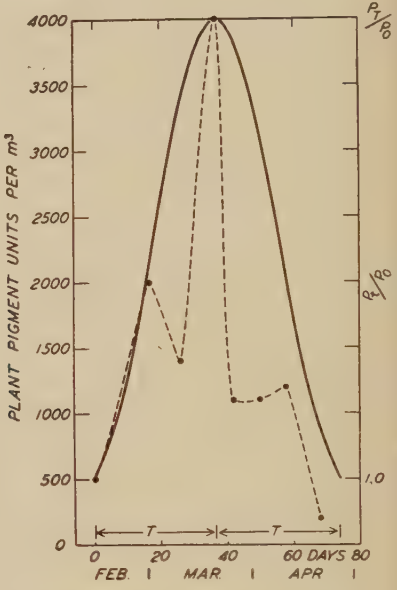

Fig. 1. Heavy line indicates the computed population curve for the spring diatom maximum observed by Harvey *et al.* in the English Channel in 1934. Broken line joins the points of observation. The computed curve was fitted to the initial and maximum populations.

where P'_{t+1} is the diatom population on the day succeeding that when it was P_t when there is no grazing. The values of e^a and a for different rates of division are given in Table 1. The *diurnal increase factor* is defined as

$$\frac{P_{t+1}}{P_t} = e^{a-b-ct-\left(\frac{1}{2}c\right)} \tag{6}$$

where P_{t+1} is the population on the day following that when it was P_t but where grazing is taking place. Obviously the diurnal increase factor will depend on both the value of a and the grazing, and will vary with time. As the value of c is small the term $\frac{1}{2}c$ can usually be neglected.

The difference between the diurnal multiplication factor and the diurnal increase factor,

$$\frac{P'_{t+1} - P_{t+1}}{P_t} = e^a - e^{a-b-ct} \tag{7}$$

will be referred to as the *diurnal grazing factor, g.* This will vary from zero, when there is no grazing, to e^a when the whole population is removed in one day. If we divide g by the diurnal multiplication factor, we obtain the *diurnal grazing fraction.*

$$F_t = \frac{g}{e^a} = \frac{e^a - e^{a-b-ct}}{e^a} \tag{8}$$

This indicates the fraction of the population removed each day by grazing and will vary from zero, when there is no grazing, to 1, when all diatoms are removed in one day. It will be seen that equations (5),

(6), (7), and (8) are independent of the actual population as only ratios must be known and therefore do not tell us anything about the actual numbers of cells produced or consumed, but only the fractions or ratios.

If the fraction of the population removed by grazing each day is constant, that is, $c = 0$, and if $(a—b)$ is positive,

$$\frac{P_t}{P_0} = e^{(a-b)t}$$

and the population will continue to increase indefinitely. The effect of constant grazing upon the population curve is to indicate an *apparent* division rate slower than is actually the case. If b is only slightly smaller than a, the population will increase very slowly. Although many cells may be formed each day, an almost equal number are consumed by the grazers.

When $a = b + ct$, the number of cells produced is equal to that consumed. Under these circumstances the production may be large but $\frac{dP}{dt}$ is zero. If a is less than $b + ct$, the population will decrease, although production of new cells continues.

At the point of maximum population, $a = b + cT$. Therefore, $e^{a-b-cT} = 1$, and from equation (7) we can obtain the grazing factor, g_T.

$$g_T = e^a - 1.$$

From equation (8) we can determine the balancing grazing fraction, F_T.

$$F_T = 1 - \frac{1}{e^a}$$

From these it can be seen that the grazing at any maximum is determined only by the rate of division of the diatoms. The values of these expressions for different rates of division are shown in Table 1. (The values of a and F_T are also shown in Figure 2.) For a population dividing once each day, 0·5 of the population must be removed if the population is to remain constant. For slower division rates, smaller fractions must be removed to balance the production. It should again be noted that these conclusions are independent of the actual population.

Table 1.

Number of days for each division ..	0·75	1·0	1·5	2·0	2·5	3·0
Diurnal multiplication factor, e^a ..	2·52	2·0	1·59	1·41	1·32	1·26
Diurnal multiplication index, a	·924	·693	·462	·347	·277	·231
g_T	1·52	1·0	0·59	0·41	0·32	0·26
F_T	0·60	0·50	0·37	0·29	0·24	0·21

The initial grazing factor g_0 and grazing fraction F_0, can be determined from equations (7) and (8).

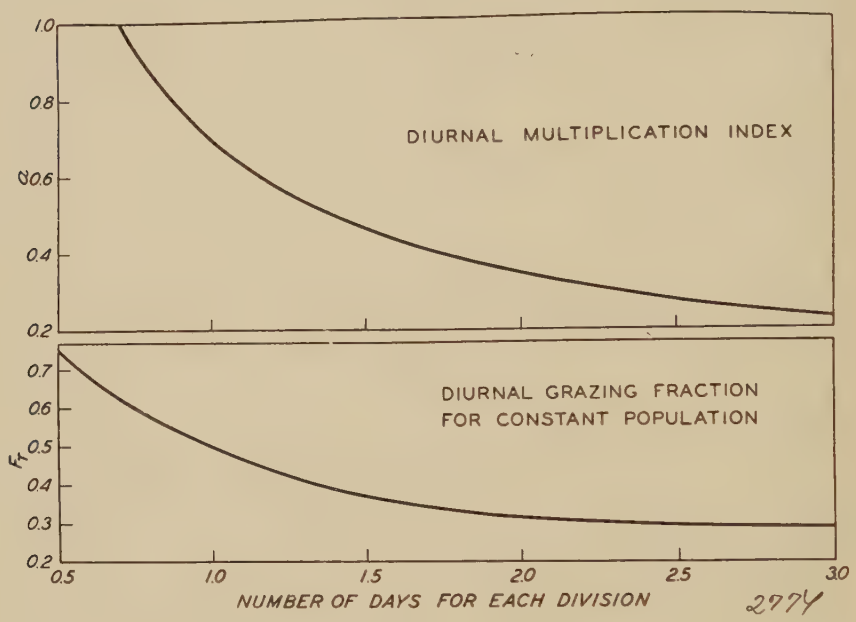

Fig. 2.

Upper Curve. The diurnal multiplication index, *a*, corresponding to different rates of division.

Lower Curve. The diurnal balancing grazing fraction necessary to equal the production and thus maintain stationary populations for different rates of division.

$$g_0 = e^a - e^{a-b}$$

$$F_0 = 1 - \frac{e^{a-b}}{e^a}$$

On the basis of the discussion thus far, if we know the values of T and the ratio $\frac{P_T}{P_0}$ we can plot the form of the population curve and determine the values of $(a—b)$ and c. If a is known for the species under consideration under the given environmental conditions, we can determine g_0 and g_T and F_0 and F_T. If the absolute values of P_T and P_0 are known, the population curve will show the actual change in population.

Application of Equations.

Solutions of equations (2), (3) and (4) can be obtained when we know the ratio of the maximum population, P_T, and the initial population, P_0, and the time interval T, required for the development of the maximum population. At the maximum, $\frac{dP}{dt} = 0$, and from equation (2)

$$a-b-c\mathrm{T}=0.$$

$\frac{P_T}{P_0}$ is known and therefore equations (2) and (3) or (4) can be evaluated. From these we can obtain the values of $(a-b)$ and c, and can construct the relative population curve for the time interval $t=0$, to $t=2\mathrm{T}$. The shape of the curve depends, of course, upon the values of $\frac{P_T}{P_0}$ and T (Fig. 1).

As an example let us consider the data given by Harvey *et al.* for the spring maximum in the English Channel in 1934. Using the values for the diatom population expressed as plant pigment units per cubic metre (Harvey *et al.*, Fig. 7, p. 417) we find an eightfold increase in the population in approximately 37 days, with a subsequent decrease. The maximum population occurred late in March. On the basis of these data we can substitute in equations (4) and (2), and solve for the values of $(a-b)$ and c.

$$\ln 8 = (a-b)37 - \frac{1}{2}c\,37^2$$

$$a-b = 37c.$$

From these we obtain $a-b=0{\cdot}1123$, and $c=0{\cdot}003038$. Using equation (4) we can then construct the population curve shown in Figure 1. The use of plant pigment units in this calculation introduces the assumption that the plant pigment content of the individual cells is constant over the time interval 2T, or that instead of considering that the increase is due to the formation of "additional cells", we read "formation of plant pigment units". The plots of the computed population and the observed population, expressed in plant pigment units per m^3., do not appear to agree very well. However, it should be remembered that the form of the computed curve is determined by only the initial and maximum populations. Furthermore the computed curve is based on the assumption that the grazing increases regularly while the observations show that the zooplankton fluctuated considerably although there was a general increase during the interval under consideration. Harvey *et al.* consider that the diatoms during this period were dividing once every 36 hours; therefore $e^a=1{\cdot}59$, $a=0{\cdot}462$, $g_T=0{\cdot}59$ and $F_T=0{\cdot}37$. The initial grazing fraction, F_0, is 0·30. That is to say, there has been about a 25 % increase in the fraction of the population removed each day in the 37 days between the start and the time of maximum population.

Total Production and Yield.

The production of cells by division varies with time, depending upon the population, the rate of division and the grazing. The total production over and above the initial population, P_0, is given by the following equation:—

$$\text{Total production} = C_t = aP_0 \int_0^t e^{(a-b)t - \frac{1}{2}ct^2}\, dt$$

When integrated this equation takes the form

$$C_t = \frac{aP_0}{\sqrt{c/2}}\, e^{\frac{(a-b)^2}{2c}}\, \frac{\pi}{2} \left\{ \varphi\left(\sqrt{ct/2} - \frac{a-b}{2\sqrt{c/2}}\right) + \varphi\left(\frac{a-b}{2\sqrt{c/2}}\right) \right\}$$

where φ is the probability integral. The numerical values of φ may be obtained from published tables (for example, Peirce, 1929, pp. 116—120).

As $e^{\frac{(a-b)^2}{2c}} = \frac{P_T}{P_0}$, this equation may be written

$$C_t = aP_T \frac{0.886}{\sqrt{c/2}} \left\{ \varphi\left(\sqrt{ct/2} - \frac{a-b}{2\sqrt{c/2}}\right) + \varphi\left(\frac{a-b}{2\sqrt{c/2}}\right) \right\} \qquad (9)$$

Substituting in equation (9) the values from Harvey *et al.* found on page 217, and adding $P_T = 4000$ plant pigment units per m^3., and assuming various values of a, we obtain the values in Table 2.

Table 2.

	Total Production			Population	Population Increment	Yield		Phosphorus Consumed	
	Plant pigment units /m.^{3}			Plant pigment units /m.^{3}	Plant pigment units /m.^{3}	Plant pigment units /m.^{3}		mg./m.^{3}	
t (days)	$a = .693$	$a = .462$	$a = .347$			$a = .693$	$a = .462$	$a = .693$	$a = .462$
0	0	0	0	500	0	0	0	0	0
10	6,200	4,200	3,100	1,320	820	5,380	3,380	0·69	0·47
20	19,400	12,900	9,700	2,580	2,080	17,320	10,820	2·06	1·43
30	41,500	27,700	20,800	3,710	3,210	38,290	24,490	4·61	3·08
37	60,300	40,200	30,200	4,000	3,500	56,800	36,700	6·70	4·47
40	68,500	45,700	34,300	3,940	3,440	65,060	42,260	7·61	5·08
50	93,500	62,400	46,800	3,100	2,600	90,900	59,800	10·40	6·94
60	110,100	73,500	55,200	1,750	1,250	180,850	72,500	12·22	8·18
70	118,500	79,000	59,800	770	270	118,230	78,730	13·18	8·78
74	120,700	80,500	60,400	500	0	120,700	80,500	13·40	8·95

Harvey *et al.* determined the relationship between the plant pigment units and the phosphorus content of the diatom catches, and from the drop in the dissolved inorganic phosphorus during the spring outburst calculated the production to be between 75,000 and 100,000 plant pigment units per m^3. The computed production for $a = \cdot 462$, namely 80,500 units, agrees excellently with these estimates. Harvey *et al.* assumed that there had been no significant regeneration of phosphorus during this interval. If there had been some regeneration, the production computed from the phosphorus consumption would be somewhat too low and possibly the value of 120,700 plant pigment units per m^3., corresponding to diurnal division, may be closer to the

actual production. In order to apply the production equations with certainty more must be known concerning the division rate of plankton diatoms.

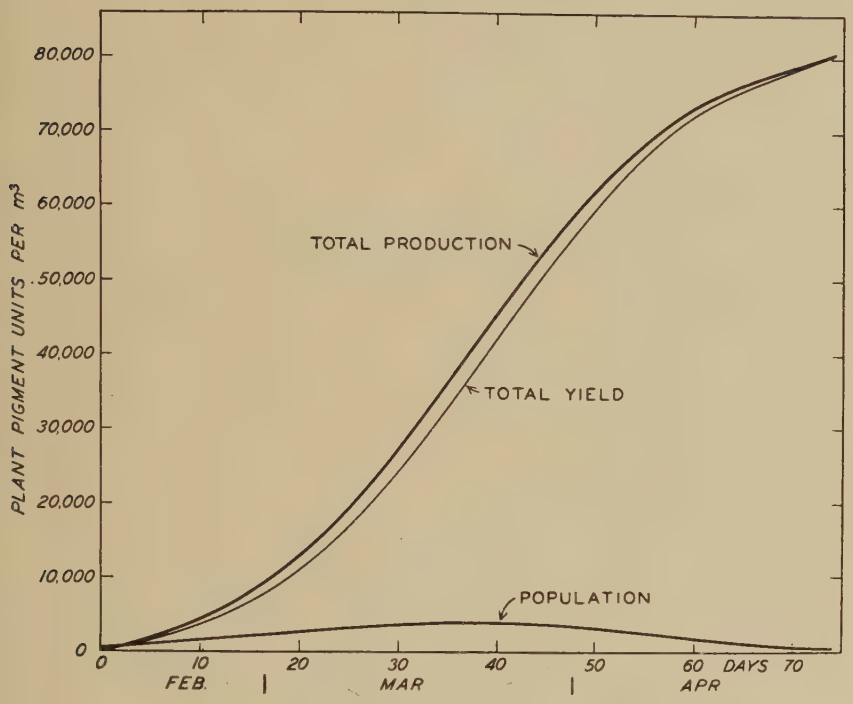

Fig. 3. Computed total production, total yield, and population based on the observations of Harvey *et al.* The total yield represents the total amount which has been removed by grazing. Assumed division rate once every 36 hours.

Population, Production and Plant Nutrients.

From the data in Table 2, and Figure 3, it is obvious that the total production over any appreciable period is much greater than the population at any time. It is therefore impossible to obtain much, if any, correlation between the population and the change in the concentration of plant nutrients. If, as postulated by Cooper (1933), Harvey *et al.*, and Cooper (1938), the process of regeneration is relatively slow, the total production curve should show a close agreement to the depletion of nutrients. In Figure 4 are shown the observed depletion and the depletion computed from the total production assuming a division rate of once every 36 hours for the interval covering the spring outburst. The observed depletion is based on the assumption that the initial phosphate phosphorus was 16 mg./m³. The

relationship used is that 9,000 plant pigment units are equivalent to 1 mg. of phosphorus. The relationship established here is obviously more reasonable than any attempt to relate the phosphorus depletion to the population. Only where grazing is very slight will there be any relation between the population curve and phosphorus consumption.

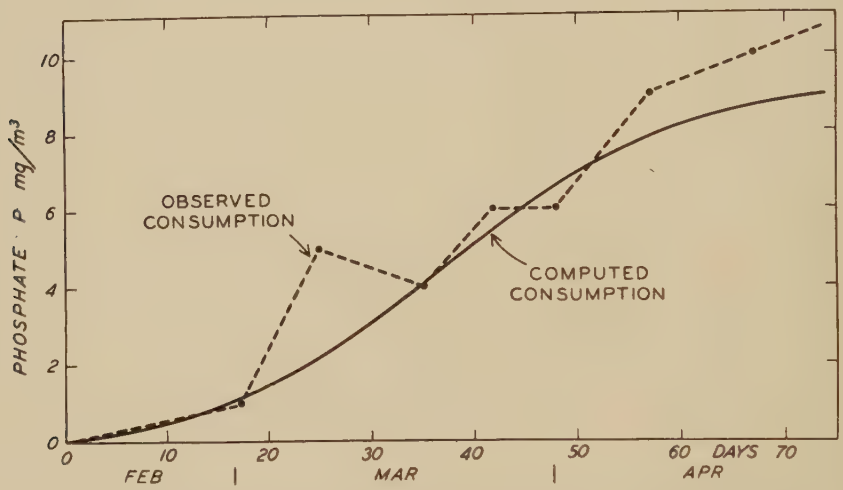

Fig. 4. Observed and computed phosphate phosphorus consumption. The observed consumption represents the average for the water column, assuming an initial content of 16 mg./m³. Assumed division rate once every 36 hours.

Grazing Fraction and Filtration Volume.

Most, if not all, of the larger zooplankton organisms consume diatoms. Although extreme differences in the relative sizes of various diatoms and grazers may make some of the diatoms unsuitable as food material, the plankton grazers seem in general to be indiscriminate feeders. That is, copepods and other zooplankton grazers probably remove particulate matter from the water regardless of whether or not they are able to digest this material. Experiments on the feeding behaviour of certain copepods and mysids (Lucas, 1936; Fuller and Clarke, 1936; Fuller, 1937) indicate that individuals of any species filter, that is, remove the diatoms from, approximately the same quantity of water in a given interval. In the present connexion it is not necessary to know the actual mechanism by which these organisms capture and ingest the diatoms. Also it is not known whether the diatoms are completely removed from a given volume. However, the investigations mentioned above indicate that the removal of diatoms can be expressed as a filtration capacity which is equivalent to the volume from which all diatoms have been removed in a given time interval. The filtration capacity depends upon the type of organism,

the temperature, and possibly the size of the diatoms and environmental factors such as light intensity (Fuller, 1937). The filtration capacity of any species shows some variation under a given set of conditions but it is apparently independent of the diatom population. For example, the experiments of Fuller (1937) were carried out with suspensions of *Nitzschia closterium* varying from 1,875 to 410,000 cells per ml. The computed filtration capacity per copepod, in this case *Calanus finmarchicus*, at 13°C. expressed as ml. per day, varies only from 0·65 to 1·76 with an average of 1·18[2]). Lucas (1936) does not give the filtration capacities but these can easily be computed from the data given. His results also indicate that the filtration capacity is independent of the diatom population. Lucas found that the filtration capacity decreased somewhat with time, but Fuller's experiments do not support this observation. It should be pointed out, however, that the diatom cultures used by Lucas and Fuller were generally of much greater concentrations than are found in nature. The point to be emphasized is that for any species under a given set of environmental conditions there is apparently a characteristic filtration capacity which is independent of the number of diatoms present in the water.

In the discussion of the relationship of grazers to the change in diatom population, no mention was made of the feeding mechanism or behaviour of the grazers. The expression introduced was the "grazing fraction", that is, the fraction of the population removed in one day. If the grazing organisms filter a given volume of water per day, they will remove the diatoms from a certain fraction of the water mass. This fraction is independent of the diatom population and therefore bears a definite relation to the grazing fraction. Therefore, if the zooplankton population remains unaltered, the grazing fraction will be constant. The relationship between the number of grazers, the individual filtration capacities, and the grazing fraction can be shown in the following way:—

Let N be the number of grazers per litre, and v be the filtration capacity, that is, the volume in litres, filtered by each organism per day. Let us assume that all the diatoms are removed from the water filtered by the grazers, that is, from the volume Nv, and that the population is kept evenly distributed by mixing. Therefore

$$dP = N_t v \, P dt.$$

By comparison with equation (1) it follows that $N_t v = b + ct$.

Therefore the total grazing volume can be determined in any case where b and c are known. At the population maximum, $a = b + cT$, therefore, $N_T v = a$. That is, the total filtration volume necessary to balance production depends only upon the rate of division and is equal to a.

[2]) The filtration capacities, W24, given by Fuller (1937) are in some cases incorrectly computed so that the average value in Table I, p. 234, should be 1·18 instead of 1·09.

The expression for the grazing fraction can then be written

$$F_t = 1 - \frac{e^{a - N_t v}}{e^a},$$

and for the balancing grazing fraction,

$$F_T = 1 - \frac{1}{e^{N_T v}} = 1 - \frac{1}{e^a}$$

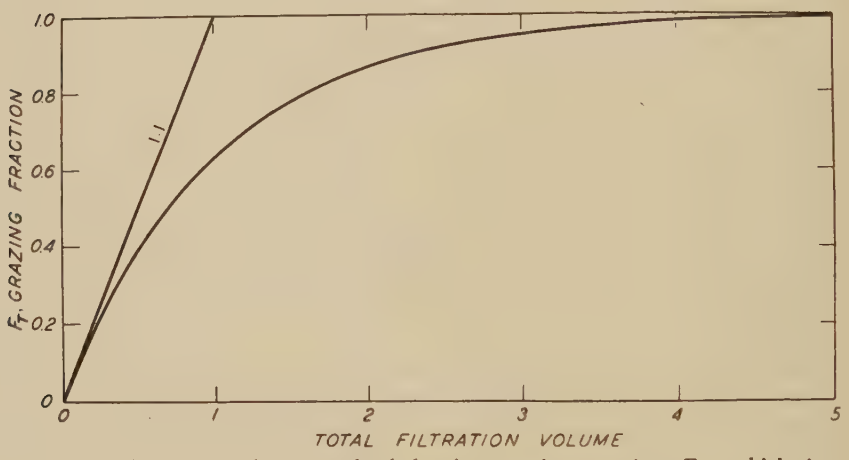

Fig. 5. The relation between the balancing grazing fraction, F_T, which is the fraction of the population which must be removed each day in order to balance production, and the total filtration volume, $N_T v$. The latter is the total volume filtered each day by the zooplankton grazers.

It may also be seen that the balancing grazing fraction does not bear a linear relation to the filtration volume. In order to remove all the diatoms in one day, $N_T v$ would have to be infinite. In Figure 5, the relationship between $N_T v$, and the balancing grazing fraction is shown. The straight line shows the relationship which would exist if it was a direct one, that is, if $F_T = N_T v$. It is obvious that the efficiency of feeding falls off as the number of grazing organisms increases. From the foregoing, it is obvious that the grazing will not vary directly as the population of grazers. If we assume that the filtration volume per individual is constant, the form of the curve in Figure 5 represents the relation between the grazing fraction and the number of individuals.

If Nv is constant, equation (1) may be written

$$dP = P\,(a - Nv)dt$$

and when integrated,

$$\frac{P_t}{P_0} = e^{(a - Nv)t}.$$

In experimental investigations of the filtration capacity this equation

may be used where the number of animals is constant and a is known. If the diatoms are not dividing, $a = 0$.

The data of Harvey *et al.* indicated that the diatoms divided once in 36 hours, and that $F_0 = 0{\cdot}30$, and $F_T = 0{\cdot}37$. The corresponding values of Nv are then 0·35 and 0·46. When dealing with a mixed zooplankton population, as in this case, the individual filtration capacities for the different species should be known as well as their relative numbers so that a weighted value of Nv could be determined. Our present lack of knowledge of the values of v for different species makes such a procedure impossible. However, we can introduce the known filtration capacity for a given species and evaluate the intensity of grazing in terms of the number of the given species per litre. At a temperature of 8°, approximately the temperature in the English Channel during the spring, Fuller (1937) found that *Calanus finmarchicus* had a maximum filtration capacity of nearly 3·0 ml./day. If we introduce this in the values of Nv given above we find $N_0 = 117$ and $N_T = 153$. That is, the initial grazing was equivalent to that of 117 *Calanus* per litre, and the grazing at the population maximum was equivalent to 153 *Calanus* per litre. This estimate is much greater than the total number of animals per litre found by Harvey *et al.*[3]). During the interval of the spring diatom development the number of animals varied from about 5 to 20 per litre. Of these about one-half were copepods. Furthermore, the copepods were of species smaller than *Calanus* and might be expected to have smaller filtration capacities. It appears, therefore, that the equivalent grazing population in terms of *Calanus* is much too high. This discrepancy can be accounted for if, first, the filtration capacity introduced is too small; second, the diatoms and grazers are concentrated in the upper part and not evenly distributed through the water column (as assumed by Harvey *et al.*); or, third, certain zooplankton forms with large filtration capacities escaped capture in the net.

As far as the filtration capacities are concerned, little can be added. Fuller and Clarke (1936) obtained values of 5·6 ml./day for *Calanus* and Fuller (1937, p. 243) states that Harvey found values as high as 50 and 100 ml./day, but Fuller considers these values untrustworthy. Lucas (1936) used the copepod *Eurytemora hirundoides* and cultures of *Nitzschia closterium.* Omitting two high values (0·34 and 0·70) his data give an average filtration capacity per copepod of 0·12 ml./day with range from 0·07—0·19. Using the mysid, *Neomysis vulgaris,* Lucas's data show, on the basis of 20 experiments in sea water, an average filtration capacity of 11·5 ml./day with a range from 3·0 to 27·0 ml./day. It is hoped that further investigations will be undertaken to determine the characteristic filtration capacities for given species grazing upon different types of food material under various environmental conditions.

[3]) The values shown in several of the figures in this reference should be multiplied by 10, See errata to Vol. 20, J. M. B. A.

Additional evidence that grazing is independent of the diatom population is afforded by the observations of Harvey *et al.* who found an excellent agreement between the diatom population and the number of faecal pellets per copepod plus copepodite. Furthermore, they noted that during the spring diatom maximum, when there was the maximum ratio of faecal pellets, that the pellets contained large quantities of plant pigments. This they interpreted as indicating that the animals were consuming so much food that they were unable to digest all the food material it contained. Fuller (1937) found that the faecal pellets of *Calanus* used in his feeding experiments contained about one-half the nitrogen which had been ingested in the form of diatoms. Fuller interprets this to mean that the copepods are unable to utilize more than one-half of the organic matter contained in the diatoms. On the other hand it may merely indicate that the copepods were over-feeding, in face of high concentrations of diatoms upon which they were grazing.

Diatom and Zooplankton Maxima.

It has been shown that the balancing grazing fraction necessary to maintain a constant population is determined only by the division rate of the diatoms. Whenever the grazing is in excess of this value, F_T, the population will decrease; if less, it will increase. The typical bell-shaped population curve assumes an increasing grazing fraction over the interval 2T. Nothing has been stated concerning subsequent relationships between the population and the grazing. At the time 2T the population has been reduced to its initial value, P_0, and yet there is relatively intense grazing. If this intense grazing is maintained the population will continue to decrease. However, when the population of a given water mass drops below a certain limit it cannot supply much food to the zooplankton forms and consequently we may assume that they either die, are removed by predators, cease feeding, or, if they are able to do so, move out in search of new food supplies. If through these or any other causes, the grazing fraction drops below F_T, the diatom population is able to increase once more. As the population increases the available food supply improves and the production increases, which may lead to the re-establishment of the zooplankton and consequently increasing grazing once more. In this manner the cycles of minima and maxima in the diatom population characteristic of the summer and fall months may be controlled by fluctuations in the grazing. Steemann Nielsen (1937) and others have advanced many hypotheses to account for the apparent fact that zooplankton maxima *follow* diatom maxima during the vegetative season. From the above reasoning it appears that diatom maxima *follow* a decrease in the grazing, that is, generally speaking, a decrease in the zooplankton. Although it may be argued that the increase in grazing will rarely, if ever, be so regular as assumed in equation (1), the relationship between F_T and the division rate is quite

independent of these assumptions. Examination of the data given by Harvey *et al.* and similar data from other sources has shown that in practically all cases where there is a marked decrease in the zooplankton, there is an increase in the diatom population.

Within recent years considerable attention has been given to the "animal exclusion" hypothesis set up by Hardy (1935—6). From the preceding discussion it can be seen that the probability of a high zooplankton population occurring simultaneously with a dense diatom population is extremely small. Suppose that a large diatom population has developed and that the number of zooplankton grazers is rapidly increased several fold due to the development of a new generation of young, or to the intrusion of an outside population. The grazing will be greatly in excess of the production and consequently the diatom population will decrease abruptly.

For example, let us assume that there is a population of 1,000,000 diatoms per litre which are dividing once each day and that the grazing just balances the production. That is, the population is stationary and the production is 1,000,000 cells per litre per day. Suppose that by some means the total filtration volume is doubled or increased fivefold, and then remains constant. Although the diatoms continue to divide, the population will drop off rapidly, as shown in Table 3. For the initial conditions $a = \cdot 693$, $Nv = \cdot 693$ and $F_0 = \cdot 50$.

Table 3.

Time in days	Population (cells per litre)	
	Filtration volume doubled $Nv = 1 \cdot 386$, $F = 0 \cdot 75$	Filtration volume increased 5-fold $Nv = 3 \cdot 466$, $F = 0 \cdot 969$
0	1,000,000	1,000,000
1	487,000	62,000
2	237,000	3,900
3	106,000	240
4	56,000	15
5	27,000	<1

From this it is obvious that any large increase in the grazing associated with an increase in the number of grazers will reduce the diatom population very rapidly. When samples are obtained at intervals of more than a few days there is little likelihood of finding a large zooplankton population associated with a dense diatom population. The development of dense diatom populations can only take place when the grazing is less than the production of new cells. If the number of zooplankton forms is such that the grazing is in excess of the production the population must always decrease.

The discussion of the relation between grazing and the changes in diatom population has been restricted to the simplest assumptions so that the basic ideas would not be obscured. Curves to represent the population changes more closely could be obtained by introducing refinements, such as a variable multiplication index, *a*, and fluctuating

values for the grazing. However, if such adjustments were made they could only apply to a single set of data and it is considered that more definite knowledge concerning the rate of division of diatoms and the nature of zooplankton grazing is necessary before such exact adjustments would be justified. Besides knowledge concerning the effect of physical and chemical factors upon the division rate, the possible effect of such factors on the size and cell contents of the diatoms should be investigated. The latter information is necessary if the computed production or yield of diatom cells is used as a measure of food supply. Furthermore, much more information concerning the grazing of zooplankton forms is essential before more exact calculations are justified.

Acknowledgements.

I wish to express my thanks to Dr. H. U. Sverdrup, Director of the Scripps Institution of Oceanography, and to my associates on the staff for their suggestions and help. Assistance in the preparation of these materials was furnished by the personnel of the Works Progress Administration, Official Project No. 665—07—3—141.

Summary.

1. The importance of grazing by zooplankton organisms in the control of diatom populations in the sea is emphasized. The discussion deals especially with the development of a large population in a given water mass and its subsequent disappearance due to grazing.

2. The treatment is based on the following assumptions; first, that the diatoms continue to divide at a constant rate; second, that the fraction of the population removed each day by grazing increases.

3. An equation is developed which represents the form of the diatom population curve. The shape of this curve is determined by the ratio of the maximum to the initial population and the time required for the development of the maximum population.

4. If the division rate of the diatoms is known, it is possible to determine the grazing fraction. The grazing fraction is the fraction of the population removed in one day.

5. An equation is developed for computing the total production of diatoms for any interval between the initial time and the time when the population passes through the maximum and returns to the initial value.

6. The equations developed are applied to observations from the English Channel for the spring of 1934. The computed production agrees excellently with estimates based on phosphate utilization.

7. The relation between the grazing fraction and the total filtration volume is shown. The total filtration volume depends upon the type of grazing organisms and their capacity to filter a given volume of water per day regardless of its food content.

8. The maxima and minima in the diatom population during the vegetative period are shown to be related to the fluctuations in the grazing fraction.

9. The small probability of encountering a large zooplankton population simultaneously with a dense phytoplankton population is shown.

10. The necessity for more adequate knowledge concerning the division rates of plankton diatoms and the effect of environmental factors on these is pointed out. It is also shown that more information is necessary concerning the feeding mechanism of zooplankton grazers and that determinations of their filtration capacity under various environmental conditions are essential.

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After this paper had been submitted, the author's attention was drawn to a contribution by H. W. Harvey, entitled "Note on selective feeding by *Calanus*". (Journ. Mar. Biol. Assoc., Vol. 22, pp. 97—100, 1937). Harvey's data definitely show that the filtration capacity of *Calanus* is influenced by the size of the diatoms being consumed. For larger diatoms, the filtration capacities are much greater than those obtained by Fuller (1937), for *Calanus* feeding upon *Nitzchia closterium*, and which were used in calculating the equivalent grazing population (page 14). Harvey's values bring the calculated population much closer to the observed zooplankton population. Although these observations show that the filtration capacity depends upon the size of the diatoms, they do not necessarily invalidate the assumption that the volume of water filtered in unit time by any species of grazers is constant under a given set of environmental conditions. The variations can be explained on the assumption that the efficiency of filtration increases with the size of the diatoms. Furthermore, if the diatoms are present in colonies or chains the efficiency will be greater.

Étude sur les Variations de Fertilité des Eaux Méditerranéennes.
Climat et Nanoplancton à Monaco en 1937—38.

Par

Francis Bernard,
Institut Océanographique, Paris.

Introduction.

LE but du présent travail est de comparer les résultats obtenus à Monaco en 1937 avec ceux de 1938. Ces deux années, bien différentes par le climat local, fournissent une expérience naturelle sur les relations entre les facteurs météorologiques, la nature du nanoplancton et son volume total.

Les résultats obtenus complètent deux mémoires précédents, auxquels je renvoie une fois pour toutes: l'un relatif au cycle de fertilité à Monaco et à Banyuls en 1937 (3); l'autre concernant les échanges saisonniers de liquide en 1938 (4). On trouvera aussi l'indication des Coccolithophorides les plus communs dans une récente note (5).

La technique suivie, détaillée dans la première étude ci-dessus, ne sera décrite ici que très brièvement. Les prises d'eau sont faites à Monaco, une fois par semaine à la station II (à 10, 50, 200 et 350 m.) et deux fois par mois à la station III (à 500 et 1.000 m.). Le nanoplancton (compris comme totalité des Protistes contenus dans l'eau) est fixé au formol neutre et dénombré par sédimentation au dessus d'un microscope inversé. Sa densité est estimée en volume des Protistes par litre d'eau, d'après les dimensions moyennes des espèces les plus abondantes. Les Flagellés calcaires en forment la partie essentielle (voir tableau II, p. 232), grâce à l'importance de *Coccolithus fragilis*, dont les individus représentent en moyenne plus de 70 % du groupe.

Les données météorologiques sont fournies par le poste du Musée de Monaco. J'ai disposé ainsi de chiffres sûrs à propos des facteurs

suivants:— pluie, vitesse des vents, nombre d'heures d'insolation; température, teneur en phosphates, nitrates et nanoplancton dans 230 échantillons d'eau pour chaque année; proportion des espèces de Diatomées, Coccolithophorides et Silicoflagellés. Les Dinoflagellés n'ont pas été déterminés, leur volume moyen est d'ailleurs faible à Monaco. Les petits Flagellés (Chlamydomonadines, Chrysomonadines, Cryptomonadines) sont communs, mais leur détermination n'a pas été abordée étant donné le but surtout quantitatif poursuivi dans cette étude.

D'autres données intéressantes se rapportent à l'activité solaire et la transparence marine. Malheureusement, il n'existe pour les Flagellés méditerranéens aucune recherche sur l'optimum de lumière comparable à ce qui a été fait pour certaines Diatomées nordiques. Depuis Octobre 1938, un luxmètre à cellules photo-électriques fonctionne à Monaco, entre 0 et 100 m. de profondeur, deux fois par mois. Sans anticiper sur la publication de ces mesures, il est possible ici d'énoncer un des résultats obtenus; la transparence méditerranéenne, beaucoup plus grande que celle des mers ouvertes, paraît dépendre surtout de la densité du nanoplancton. Profonde, peu agitée, dépourvue de marées, l'eau de Monaco ne contient de vase en suspension qu'après les rares tempêtes annuelles; le reste du temps, la transparence des couches entre 0 et 100 m. se montre d'autant plus faible que les Protistes sont plus abondants[1]).

Quant à l'éclairement solaire, seul le nombre d'heures d'insolation semble avoir quelqu'importance pour la fertilité locale en 1937 et 1938. La différence d'éclairement et de nébulosité entre les saisons est plus faible en Méditerranée qu'ailleurs; le cycle et la composition du plancton s'y rapprochent des conditions tropicales plus que de celles des océans situés aux mêmes latitudes.

Atkins (I, 1938) a montré une relation possible entre les valeurs de la constante solaire, l'échauffement et la fertilité marine. Malgré leur intérêt, ces rapports ont besoin de confirmation, car les faibles changements annuels signalés par Abbot pour la radiation solaire dépassent à peine les erreurs de mesure et sont encore contestés par beaucoup de spécialistes. Quoi qu'il en soit, j'ai pris comme indice de variation solaire les nombres relatifs de taches, que je dois à l'obligeance de M. d'Azambuja, de l'observatoire de Meudon. Ces nombres, assez comparables entre 1937 et 1938, ne m'ont fourni aucune indication intéressante au sujet des différences de densité planctonique pour un même niveau et une même durée d'insolation.

Avant d'examiner les résultats, il convient de se demander si le nombre des échantillons connus et la méthode suivie permettent une comparaison valable entre deux années différentes.

I°. Vu la rapidité des changements marins, le rythme d'une série de prises par semaine est à peine suffisant près de la surface. Au-dessous de 200 mètres, l'expérience montre que les oscillations de fertilité

[1]) Il en est tout autrement à Plymouth, d'après Atkins (1939). L'importance de la vase soulevée par la marée est très grande, et la transparence maximum a été observée lors du maximum printanier de phytoplancton.

sont moins brusques; la cadence des recherches paraît donc assez bonne pour comparer deux époques, surtout en procédant par moyennes mensuelles et annuelles.

2°. Le volume des Protistes, évalué par litre, ne donne qu'une notion très approximative de la fertilité réelle des eaux. Des êtres à vie courte, tels que les Bactéries et les plus petits Flagellés, forment une masse annuelle de substance vivante bien supérieure à celle des gros Coccolithophorides et Diatomées, dont la multiplication est beaucoup plus lente[1]). Il ne sera possible que plus tard d'attribuer à chaque Protiste son coëfficient propre de multiplication et d'activité chimique.

3°. Le poste météorologique établi à Monaco ne renseigne pas complètement sur ce qui se passe à 6 km. au large (Station II) ou à 14 km. (St. III). Par exemple, au printemps et en été, le plancton démontre par sa nature une forte dominance des courants du large, bien qu'à la côte le vent favorise les courants de sens inverse. Les pluies sont probablement plus restreintes au large, étant donné la condensation des nuages sur les hautes falaises côtières.

4°. L'amplitude des variations saisonnières d'éclairement, de salinité, de fertilité, est beaucoup plus forte dans les mers nordiques qu'en Méditerranée. Alors qu'à Plymouth ou en Norvège le maximum annuel de phytoplancton peut faire plus de 100 fois le taux minimum hivernal, ce rapport ne donne que 10 en surface à Monaco, et 4 à 6 seulement au dessous de 200 m.; on se rapproche des conditions biologiques tropicales, où les très faibles changements de la masse de Protistes semblent surtout obéir à l'agitation des eaux (voir M a r s h a l l 1933).

En conséquence, il faut être très prudent pour affirmer une différence quantitative entre deux périodes, et pour en chercher l'explication. Seuls les écarts très manifestes pourront être interprétés ci-dessous.

Comparaison des Moyennes Annuelles.

1938 a été bien moins pluvieux que 1937; l'examen des précipitations, enregistrées depuis 1905 jusqu'à 1937 à Monaco, montre que 1938 est une année anormalement sêche, alors que 1937 est un peu supérieur à la moyenne générale. Nous verrons d'ailleurs que, à tous points de vue, 1938 a été exceptionnel, et c'est 1937 qui représente l'état normal. L'insolation (tableau I) a duré 125 heures de plus en 1938, et comme l'activité solaire paraît peu différente des années antérieures, on peut dire que la mer a reçu davantage de lumière en 1938.

Le vent, agent principal de fertilité en Méditerranée, a soufflé un peu plus fort en 1938; à Monaco, on enregistre une faible prépondérance des vents du large par rapport à 1937, c'est-à-dire une importance encore plus marquée de ces vents loin de la côte. Malgré une insolation

[1]) Le rythme de division des Diatomées pélagiques en culture pure est de l'ordre d'une bipartition par cellule et par jour. Celui des *Coccolithus* ne doit pas être plus rapide, si l'on en juge par la rareté des stades de division. Les poussées de ce genre à Monaco semblent mettre plusieures semaines pour arriver au maximum.

Tableau I.

Moyennes météorologiques en 1937 et 1938 à Monaco.

	Pluie totale (mm.)	Vitesse moyenne des vents (m. sec.) venant de la côte	Vitesse moyenne des vents (m. sec.) venant du large	Insolation: nombre d'heures total	Nombre relatif de taches solaires par jour
1937	1050	0·85 m.	0·85 m.	2470	114
1938	684	0·90 m.	0·97 m.	2595	109

plus prolongée, les vents printaniers ont sans doute refroidi la surface en 1938, car en moyenne le tableau II montre une température marine plus basse qu'en 1937, sauf au niveau de 200 m. qui est très à part à divers points de vue (voir F. Bernard, 4, 1939).

La salinité n'a été mesurée que de Septembre 1937 à Décembre 1938. L'automne 1937 a présenté des eaux moins salées que l'automne 1938; vu l'absence presque totale de pluie, de Janvier à Mars 1938, on peut conclure à une salinité moyenne notablement plus élevée en 1938. C'est par ce facteur que s'explique vraisemblablement la principale différence qualitative des deux années: rareté des Diatomées en 1938, deux fois moins nombreuses qu'en 1936 et 1937 (tableau II). L'étude saisonnière démontre que très peu de Protistes sont capables de prospérer dans les périodes de salinité élevée; l'abondance de *Coccolithus fragilis* en automne à Monaco paraît surtout due à l'intolérance des autres Flagellés calcaires et des Diatomées pour l'eau de cette période, très salée au-dessous de 50 m.

En tous cas, bien des Diatomées pélagiques (*Chaetoceros, Nitzschia delicatissima, Guinardia,* etc...) ont souvent manqué en 1938, tandis que les espèces néritiques pérennes (*Thalassiothrix, Nitzschia seriata*) étaient aussi abondantes qu'en 1937. Parmi les Coccolithophorides, les formes de surface sténohalines (*Pontosphaera, Calyptrosphaera*) témoignent d'un recul en 1938, au bénéfice de *Coccolithus fragilis* qui paraît supporter parfaitement les hautes salinités (plus de 39 $^0/_{00}$ en été) des profondeurs méditerranéennes.

Ces principaux changements spécifiques étant résumés, il reste à examiner la fertilité générale de la mer, c'est-à-dire le taux des sels nutritifs et le volume annuel de nanoplancton. En théorie, l'insolation et le vent, plus grands en 1938, doivent favoriser la circulation marine et la synthèse chlorophyllienne; 1938 devrait être plus fertile que 1937. Or, s'il y a un léger accroissement des phosphates en surface (tableau II), ils diminuent relativement au dessous de 300 m., et leur moyenne d'ensemble est un peu plus faible en 1938. Quant aux nitrates, la baisse est bien plus remarquable, puisque leur moyenne n'égale que les $^2/_3$ de celle de l'année précédente.

Ici intervient une explication assez simple, la seule plausible dans l'état actuel de nos connaissances locales; j'ai établi l'importance des apports d'eau douce, pluie et ruissellement, comme source d'azote nitrique à Monaco et à Banyuls. Si l'on fait le rapport pluie : N_2 nitrique (tableau II), il se montre pratiquement le même pour les deux

Tableau II.

Comparaison des moyennes annuelles en 1937 et 1938.

(Il a été fait 49 prises d'eau entre 10 et 200 m. en 1937, 48 prises en 1938.
— 39 — à 350 m. — 38 en 1938.
— 12 — à 500 et 1.000 m. en 1937, 18 en 1938.)

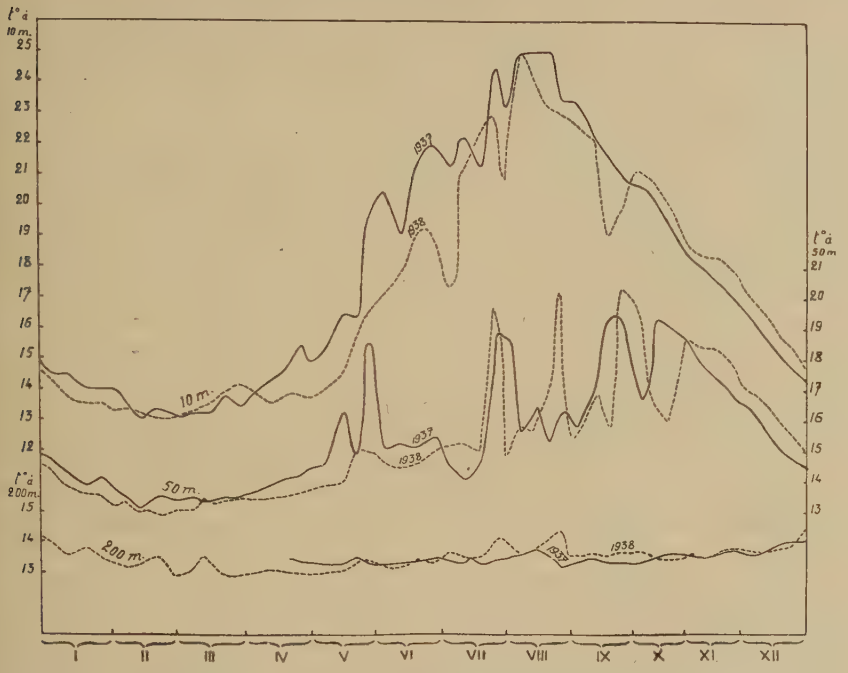
Profondeur	Année	Température	P_2O_5 mg. par m³.	N_2 nitrique mg. par m³.	Pluie / N_2	Volume de Protistes (mm³. par litre)	% en volume des Flagellés calcaires	Flagellés nus	Diatomées	Autres groupes
10 m.	37	17·95	0·41	120	8·6	0·23	52	37	8·7	6
	38	17·40	0·55	80	8·3	0·20	47	43	4·4	5·5
50 m.	37	15·60	0·35	145	7·3	0·19	54	37	5·6	7·4
	38	15·40	0·48	75	9·0	0·19	57	35	2·8	7·5
200 m.	37	13·25	0·45	200	5·2	0·18	58	33	2·4	4·5
	38	13·40	0·60	120	5·6	0·18	53	40	1·4	3·7
350 m.	37	13·50	1·5	305	3·4	0·16	57	40	0·7	5·4
	38	13·45	1·0	250	2·7	0·17	54	38	0·75	7·2
500 m.	37	13·60	2	380	2·8	0·13	60	33	0·3	3
	38	13·50	1·5	270	2·5	0·14	58	35	0·25	3·2
1000 m.	37	13·28	2·5	490	2·1	0·15	67	34	0·1	2
	38	13·22	1·7	330	2·1	0·17	60	41	0·1	2·3
Moyenne des six couches ci-dessus	37	14·57	1·2	275	3·8	0·17	58	36	3·0	4·6
	38	14·40	0·98	190	3·7	0·17	55	39	1·6	4·9

années et à chaque niveau marin; les déviations de ce rapport à 50 et 350 m. de profondeur sont de sens inverse et se compensent sensiblement dans la moyenne générale.

L'excès de nitrates par rapport aux phosphates dans les eaux côtières méditerranéennes paraît donc bien dû à l'apport des torrents et des pluies, car ces eaux douces, très riches en azote nitrique, ne contiennent pratiquement pas de phosphates[1]).

Le volume moyen du nanoplancton, compte tenu de l'imprécision des méthodes, est égal pour les deux années, à niveau comparable. Tout au plus pourrait on noter une richesse un peu plus grande à 10 m. en 1937. Cette égalité remarquable, étant donné les différences fortes d'insolation, doit être attribuée au freinage de la production par les sels nutritifs. Si l'action saisonnière de ces substances sur le phytoplancton est moins nette que ne le veulent les schémas classiques, il n'est pas douteux que le renouvellement annuel total de leur taux doit être toujours limité en Méditerranée. Malgré la réduction des nitrates en 1938, il est probable que leur quantité est restée suffisante, et c'est surtout le cycle du phosphore, plus fermé, qui est responsable des faits observés.

[1]) Bertel (1923) a montré l'existence de Bactéries fixatrices d'azote atmosphérique dans les eaux superficielles de Monaco. Il est encore impossible d'évaluer l'importance de leur apport et ses variations annuelles.



Graphique 1. Températures marines à Monaco (St. II), à 10, 50 et 200 mètres, en 1937 (——) et 1938 (-----). Les ordonnées thermiques sont décalées entre 10, 50 et 200 mètres pour la clarté de la figure.

Principales Différences Saisonnières.

Pour simplifier la comparaison entre les deux années, les variations saisonnières seront représentées sous forme de *moyennes mensuelles* (graphique 2), à l'exception de la température, dont l'examen détaillé offre plus d'intérêt (graphique 1). On abordera plus loin le problème spécial des grands maxima localisés du nanoplancton, souvent peu apparents dans les moyennes mensuelles car ils sont limités à une couche restreinte et suivis généralement d'une phase très appauvrie. De plus, nos moyennes mensuelles porteront sur l'ensemble des niveaux 10, 50 et 200 m., c'est-à-dire sur les eaux éclairées. Les eaux profondes n'en diffèrent pas beaucoup, leur cycle de fertilité étant décalé d'un ou deux mois par rapport à celui des couches supérieures dont elles reçoivent les cadavres; on reverra cela dans le chapitre suivant.

a. Rappel des principaux régimes hydrographiques saisonniers.

La comparaison de 1937 et 1938 fait ressortir avec une netteté accrue trois principes déjà énoncés dans mon travail sur 1937:

1°. En Méditerranée, mer à circulation insuffisante, la fertilité dépend étroitement de l'activité des échanges de liquide entre la surface et le fond.

2°. Ces échanges de liquide ont une origine assez variable suivant la répartition verticale des températures. Il est donc nécessaire d'accorder à chaque facteur météorologique un rôle particulier, variant avec la période de l'année où l'on se place.

3°. On peut appliquer assez bien en Méditerranée les règles énoncées par divers océanographes, et notamment par Wattenberg et Meyer (1936) pour la baie de Kiel; les équilibres marins dus aux salinités sont peu sensibles au vent, tandis que les stratifications de liquide provoquées par la température sont facilement rompues par un vent assez violent.

Ces principes une fois posés, il va être assez facile de les préciser pour Monaco (graphique 1).

En hiver, toute la mer est pratiquement isotherme de Janvier à Mars. La stratification des couches, basée sur les différences de salinité, est modifiée plus vite par les pluies que par les vents.

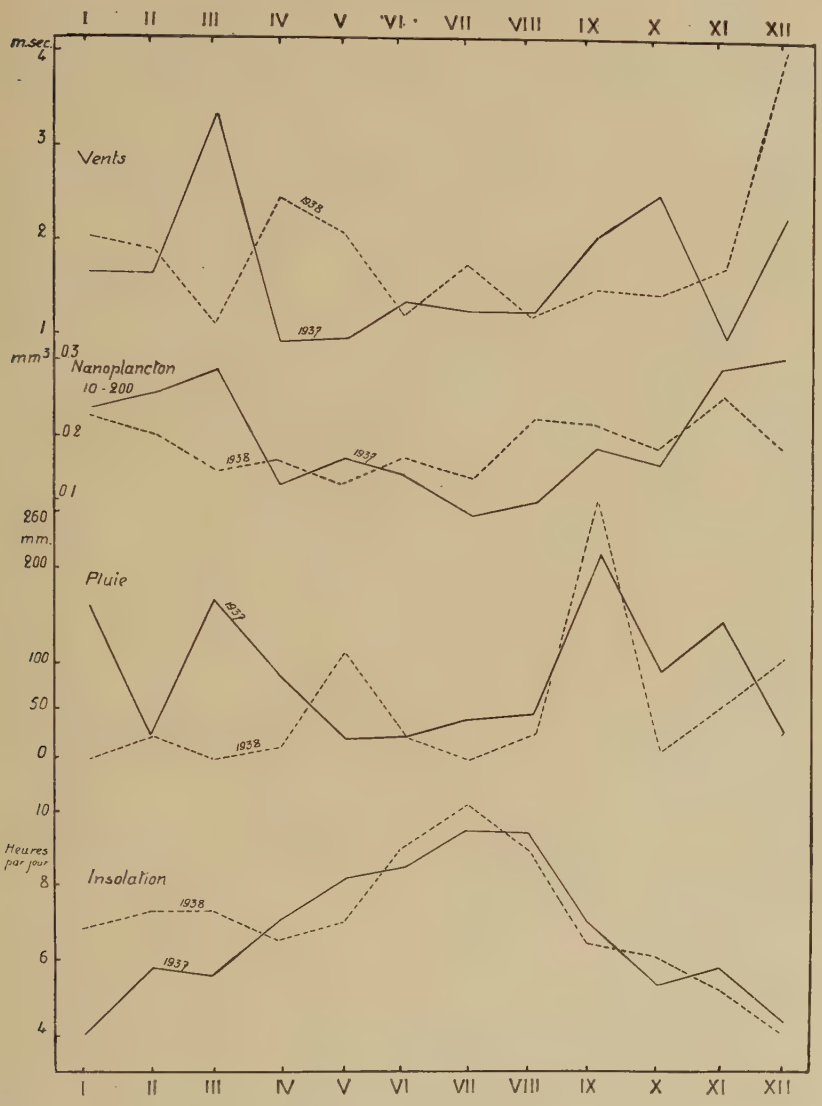
A partir de fin Mars jusqu'au début de Mai, une séparation thermique des couches commence à s'établir, l'influence du vent sur les échanges verticaux de liquide devient plus nette, aux dépens de celle de la pluie.

De Mai à Octobre, il y a un écart de plusieurs degrés entre la température à 10 m. et celle à 50 m. De temps en temps, un brusque décalage fait monter en quelques jours la température à 50 m. de 3 à 6°; il y a manifestement descente d'eau chaude de surface, d'après un mécanisme déclanché indirectement par le vent et dont voici l'allure habituelle. Quand le vent souffle, il refroidit la surface marine par évaporation. Une semaine ou deux après la chute du vent, cette surface s'est réchauffée assez pour déterminer un échange d'eau avec la profondeur, dont la température augmente brusquement. Les remontées d'eau froide à 10 m. sont assez souvent moins manifestes, sans doute parce qu'elles n'ont pas lieu suivant la verticale de la station II étudiée.

Ces échanges thermiques sont peut-être la principale source de fertilité estivale; la richesse en plancton et sels nutritifs paraît d'autant plus grande que la température du niveau considéré a été plus variable pendant le mois correspondant. Mais les circulations liquides de cette nature sont très *localisées;* l'examen des températures relevées de 1908 à 1914 à Monaco montre combien les diverses stations diffèrent quant à la date et l'intensité des décalages thermiques. Le détail des faits est bien plus compliqué pour la biologie estivale que pour les phénomènes hivernaux.

Les pluies de Septembre et Octobre, fortes mais peu durables, ne semblent pas modifier beaucoup la production de nanoplancton, sauf à 10 m. où l'afflux d'eau douce se montre tantôt favorable, tantôt nuisible aux Protistes suivant leur résistance à la dessalure.

De Novembre à Janvier, nous revenons peu à peu au régime d'hiver. La pluie reprend une plus grande efficacité, les vents, violents et particulièrement variés en direction, rendent l'interprètation de l'automne difficile, surtout en Décembre où le maximum annuel de vent paraît dépasser en 1938 l'optimum nécessaire à la circulation des substances nutritives marines.



Graphique 2. Comparaison de diverses moyennes mensuelles en 1937 (——) et 1938 (-----). De haut en bas: vents (vitesse moyenne en mètres-seconde); nannoplancton (volume en millimètres-cube par litre, moyenne entre 10, 50 et 200 mètres); pluie (totaux mensuels en millimètres); nombre d'heures d'insolation (moyenne par jour pour chaque mois).

b. Ecarts mensuels moyens entre 1938 et 1937. (graphique 2).

Janvier. Bien que 1938 soit favorisé par une insolation supérieure, des vents plus forts, une plus haute teneur en phosphates, le nanoplancton n'est pas plus grand qu'en 1937. Cela tient à l'absence de pluie, ralentissant les échanges de salinité entre les couches.

Février. La pluie est très faible pendant les deux années, mais l'insolation reste plus forte en 1938, d'où salinité anormalement élevée. Le nanoplancton, déjà peu abondant en Janvier, baisse encore, tandis qu'en 1937 il augmentait légèrement.

Mars. Bien moins de pluie, de vent et de Protistes en 1938.

Avril. Le vent est beaucoup plus fort en 1938, mais la pluie faible et l'insolation un peu inférieure déterminent un plancton à peine plus élevé qu'en 1937.

Mai. Le nanoplancton de 1938 est un peu plus rare, malgré le vent et la pluie favorables. La cause en est dans l'installation du régime estival, dont les oscillations thermiques à 50 m. étaient beaucoup plus accusées en 1937 (graphique 1).

Juin. Conditions très analogues pour les deux années; vent, températures à 50 et 200 m., quantité de Protistes sont comparables. Qualitativement, le manque de Diatomées pélagiques en 1938 a déjà été signalé ci-dessus.

Juillet. Davantage de nanoplancton en 1938, surtout à 200 m., ce qui est en bon accord avec l'oscillation de température à ce niveau. On notera aussi le vent et l'insolation plus actifs en 1938.

Août. Ascension thermique à 50 et 200 m. beaucoup plus forte en 1938; plancton des mêmes couches deux fois plus riche que l'année précédente.

Septembre. En 1938, bien que le vent noté à Monaco soit moindre, les changements de température en profondeur sont un peu plus accentués qu'en 1937, et le plancton profond est légèrement supérieur. En surface, il y a au contraire moins de plancton, sans doute à cause de l'excès de pluie.

Octobre. Mois assez mal connu, car en fin d'Octobre des deux années l'état de la mer a empêché les prises d'eau. Il semble y avoir en moyenne un peu plus de Protistes en 1938, mais sans certitude.

Novembre. En 1938, davantage de vent, mais un peu moins d'insolation, beaucoup moins de pluie et de nitrates, d'où finalement une légère prédominance pour le nanoplancton de 1937.

Décembre. C'est le mois le plus difficile à interpréter, à cause de l'intensité du vent. On peut admettre qu'en 1938, deux fois plus éventée, l'eau de mer a subi une excessive agitation. Le peu d'abondance des Protistes et le contenu très spécial de l'eau du 15. Décembre 1938 (spores d'algues, champignons, vase) viennent à l'appui de cette hypothèse.

c. Conclusion.

Presque toujours suffisamment transparente et largement illuminée, la Méditerranée manque surtout de circulation verticale et d'échanges entre le fond et la surface. En hiver, ces communications sont généralement déterminées par des changements de salinité où la pluie joue le rôle principal. Le reste de l'année, le vent est plus efficace, soit comme cause de courants, soit en provoquant des variations de la température superficielle. Mais il doit y avoir une action très complexe des vents,

et leur optimum de force et de direction reste à déterminer pour chaque saison. En tous cas, comme nous l'avons montré pour Banyuls, et pour Décembre 1938 à Monaco, un vent trop violent est plutôt nuisible à la fertilité marine.

En résumé, 1938 diffère de 1937: 1°, par un retard dans l'ascension thermique, d'où maxima d'échanges verticaux et de fertilité en Juillet—Août, période généralement pauvre en Méditerranée; 2°, par la sécheresse de l'hiver, entrainant une pauvreté relative en nanoplancton malgré la forte insolation; 3°, par l'absence de vent au mois de Mars, déterminant l'absence des remontées de phosphates et des poussées planctoniques qui caractérisent habituellement cette période.

Dans l'ensemble de l'année, ces deux phénomènes, pauvreté hivernale et richesse estivale, se compensent l'un l'autre, si bien que la fertilité moyenne est la même pour les deux années. D'ailleurs, les années sèches et éventées favorisent l'insolation et la photosynthèse, mais nuisent aux échanges hivernaux par le manque de pluie; les années pluvieuses sont moins ensoleillées, si bien qu'en règle générale le nanoplancton de Monaco ne doit pas s'écarter beaucoup de la moyenne annuelle ci-dessus évaluée.

Quelques Faits Généraux sur le Cycle du Nanoplancton.

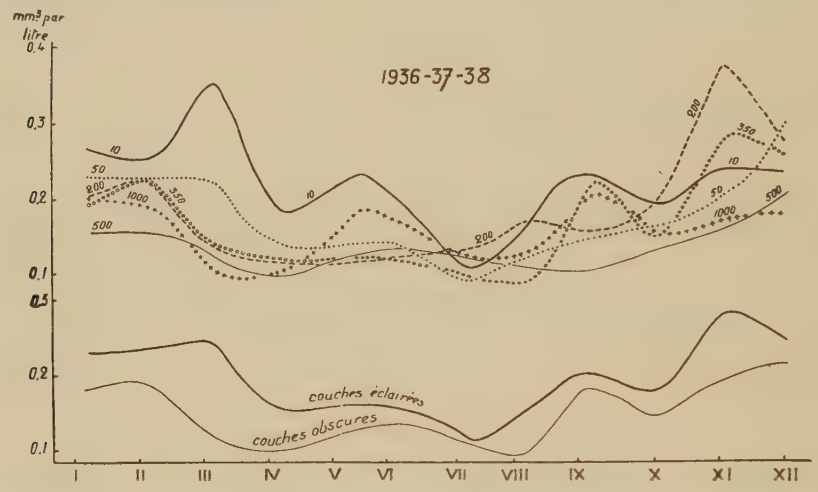
L'année 1938 apparaissant comme anormale au point de vue météorologique et biologique, il convient maintenant de résumer les phénomènes les plus caractéristiques du cycle moyen à Monaco, parmi ceux qui n'ont pas été précisés ci-dessus, c'est à dire, les différences entre les couches marines, et les dates les plus fréquentes de grande fertilité.

Pour cela, j'ai fait une moyenne entre 1936, 1937, et 1938, en accordant plus d'importance aux deux premières années à cause de leur climat relativement normal.

a. Variations mensuelles moyennes entre 10 et 1000 m. (Graphique 3).

Je me bornerai à décrire les changements les plus nets: l'explication des particularités de tel ou tel niveau exigerait une connaissance précise des conditions de la chute des cadavres et de la régénération des produits nutritifs en profondeur. Nous sommes encore mal renseignés sur la durée de ces processus. Les expériences réalisées au laboratoire, à 20—25° C., indiquent une durée d'au moins 30 à 45 jours pour la libération des phosphates et nitrates à partir de la mort d'un être planctonique. On peut admettre environ 30 jours, à la température 13° C. des eaux profondes méditerranénnes, pour la dissociation des substances protéiques simples dont se nourrissent sans doute les Flagellés et Bactéries de la zone obscure. Un maximum de Flagellés entre 200 et 1000 m. serait donc la conséquence d'un maximum planctonique un mois auparavant en surface. Quoi qu'il en soit de cette hypothèse,

nous verrons qu'elle cadre assez bien avec les grands maxima annuels, mais non avec les moyennes mensuelles, trop peu écartées les unes des autres pour appuyer une conclusion nette. De plus, la chute des cadavres est loin d'être verticale, et nous ne savons rien des maxima localisés en dehors de la station II.



Graphique 3. Variations moyennes du volume de nanoplancton (moyenne entre 1936, 37 et 38). En haut, étude de toutes les couches connues (10, 50, 200, 350, 500 et 1.000 mètres). En bas diagrammes moyens pour les couches éclairées (10 à 200) et pour les couches obscures.

La fertilité moyenne des couches s'espace verticalement d'une façon régulière en hiver, et cet écart atteint son maximum en Mars (gr. 3). Au milieu de l'année (Mai à Octobre) la surface devient plus pauvre, et les divers niveaux atteignent des fertilités très voisines les unes des autres. Il y a deux anomalies, l'une à 1000 m., où l'eau se comporte de façon assez spéciale, l'autre à 350 m. en Septembre.

Le régime d'automne est très particulier; j'en ai résumé ailleurs (4, 1939) la flore et les courants probables. La richesse des eaux à 200 et 350 m., très remarquable, est due essentiellement à des individus côtiers de *Coccolithus fragilis*. Enfin, le mois de Décembre présente chaque année le maximum annuel du niveau de 50 m., fait peu explicable dans l'état actuel des connaissances locales.

Le graphique 3 montre une certaine symétrie d'allure des courbes de part et d'autre du milieu de l'année, mais la fertilité se localise dans les couches superficielles au début, dans les couches moyennes à la fin. Comme résultante annuelle, on note une faible décroissance du nanoplancton avec la profondeur, résumée dans le tableau II. La pauvreté générale en Juillet résulte du manque simultané de vent, de pluie, et de sels nutritifs. On ne saurait invoquer l'excès d'insolation, puisque de grandes poussées planctoniques s'observent parfois en Juin et en Août.

b. Dates de quelques maxima et minima extrêmes de nanoplancton.

Les plus grandes poussées de nanoplancton à Monaco aboutissent à un volume de Protistes trois ou quatre fois plus important que la moyenne annuelle; les eaux les plus riches se rencontrent à 200 m. au milieu de Novembre (jusqu'à 0·75 mm³. au litre). Presque tous ces maxima notables sont constitués par très peu d'espèces: c'est généralement *Coccolithus fragilis* qui pullule dans ce cas, sauf en hiver, où des Flagellés non calcaires prédominent en surface. Au dessous de 100 m., ce sont toujours les *Coccolithus* qui assurent le plus d'abondance. La floraison de Diatomées en Juin n'est pas suffisante pour réaliser un volume très considérable. Le déterminisme des maxima, analysé plus en détail par ailleurs (3, 1938) est presque toujours la coïncidence de plusieurs facteurs favorables: vent, pluie, insolation etc. pendant la semaine qui précède la poussée planctonique. Pour les couches obscures, cette règle est moins souvent valable; il apparaît parfois un décalage d'un mois environ entre un grand maximum de surface et le même phénomène en profondeur. L'hypothèse de l'utilisation des cadavres formés en surface, rappelée ci-dessus, est actuellement la plus vraisemblable pour rendre compte de ce fait. Voici d'ailleurs les dates les plus régulièrement observées en 1936, 1937 et 1938.

24 au 30 Janvier: maximum ... à 10 et 50 m.
22 au 28 Février: ..... de 200 à 1000 m.
20 Mars au 1er Avril: ..... à 10 m.
30 Mai au 8 Juin: ..... à 200, 350 et 500 m.
15 au 21 Juin: ..... à 1000 m.
15 au 25 Août: ..... de 10 à 200 m.
28 au 30 Septembre: ..... à 50 et 350 m.
9 au 18 Novembre: ..... à 200 et 350 m.
15 au 21 Décembre: ..... à 50, 350 et 500 m.

La poussée de fin Mars, très superficielle, ne semble pas fournir assez de matière organique pour alimenter les profondeurs, qui restent pauvres jusqu'au début de Juin. De même, Juin et Juillet ne sont jamais très riches en surface, et il est peu probable que la zone obscure soit fertile en Août. Au mois de Septembre, une bourrasque de vent côtier est suivie d'enrichissements locaux. En automne, la surface est tantôt riche, tantôt pauvre suivant les années; on ne peut rien dire de net sur la cause des maxima des couches moyennes.

Il existe, en tous cas, une dizaine d'époques bien repérées où des maxima de nanoplancton arrivent régulièrement chaque année. Bien entendu, des poussées locales peuvent avoir lieu à d'autres dates, mais elles sont presque toujours moins abondantes que celles dont nous venons de parler.

Quant aux plus faibles minima, leur valeur n'est que le quart ou le sixième de la moyenne annuelle (soit 0·05 mm³. par litre en surface, 0·03 en profondeur). Ils se placent généralement aussitôt après les

maxima importants, ceux-ci ayant épuisé pour quelques jours la nourriture présente. L'action du plancton animal est aussi pour quelque chose dans cette réduction, mais on a peut-être exagéré l'alternance quantitative du zooplancton et phytoplancton. Ces deux ensembles, à en juger par les Copépodes trouvés dans les prises d'eau de Monaco, atteignent leurs maxima simultanément et non successivement. Le volume de nanoplancton par litre semble presque toujours supérieur à celui du zooplancton, si bien que le second n'arrive pas à supprimer complètement le premier. Les recherches de E. Steemann Nielsen (7) en Islande le conduisent à des remarques analogues.

Quelques minima de nanoplancton ont lieu, en dehors des maxima, aux époques très pauvres en sels nutritifs: Juillet, début de Septembre et début de Décembre; les phosphates surtout sont rares dans ces conditions.

En somme, le climat local d'une année particulière peut amener un déplacement notable des moyennes de fertilité mensuelles, mais ne change guère les dates des grands maxima localisés, dont le rythme paraît dépendre de quelques sautes de vent et de pluie, toujours réalisées à peu près aux mêmes époques. Les phénomènes extrêmes se répètent assez fidèlement chaque année sous le climat méditerranéen.

Résumé.

L'étude ci-dessus est l'aboutissement de trois années de recherches sur le nanoplancton à Monaco. Comme complément aux résultats déjà publiés, je compare ici la fertilité marine en 1937 et 1938, et retrace les faits les plus généraux, observés régulièrement de 1936 à 1938.

Il faut noter d'abord trois grandes différences physiques et biologiques, qui rendent l'interprétation des changements saisonniers plus délicate en Méditerranée que dans la Mer du Nord: 1°. L'insolation et la transparence de l'eau varient assez peu à Monaco. Même en hiver, les végétaux de surface disposent d'une lumière plus que suffisante pour la photosynthèse; l'opacité de l'eau est déterminée plus souvent par la masse de plancton que par la vase en suspension. 2°. L'amplitude extrême d'oscillation du volume de Protistes par litre est faible, et rappelle ce qui se passe sous les tropiques; le maximum annuel n'est que dix fois plus élevé que le minimum. 3°. Le taux des phosphates est souvent nul, et ses légères variations ne rendent pas grand service pour comprendre celles du phytoplancton. Ces principes une fois énoncés, voici les faits essentiels:

a. 1938 a été plus ensoleillé, plus éventé et bien moins pluvieux que 1937. Qualitativement, il en résulte une salinité élevée, un moindre développement des Diatomées pélagiques et de certains Flagellés, au profit du *Coccolithus fragilis* qui paraît mieux supporter ces conditions. Quantitativement, la moyenne annuelle de nanoplancton entre 10 et 1000 m. est la même qu'en 1937: malgré l'augmentation de lumière et de vent, il y a une limitation de fertilité, attribuable sans doute aux phosphates. Les nitrates, en excès manifeste sur les phosphates, proviennent en grande partie des apports d'eau douce; entre 1937 et 1938, leur rapport est égal à celui des chutes de pluie.

b. La comparaison des changements saisonniers a été faite sur les moyennes mensuelles (quatre prises d'eau par mois en général). En hiver, toute la mer est isotherme, et les échanges verticaux de liquide proviennent surtout des variations de salinité. En 1937 la pluie favorise ces échanges et le nanoplancton est plus riche qu'en 1938. En été, ce sont des changements thermiques qui assurent la circulation entre la surface et les profondeurs, et le nanoplancton abonde quand ces phénomènes sont plus intenses, comme cela s'est produit en 1938. Au printemps et en automne, le régime hydrographique est intermédiaire entre ces deux cas extrêmes et les différences de fertilité obéissent à des causes plus complexes. En moyenne, le vent joue un rôle important comme source de courants et comme action sur les échanges de température: les mois peu éventés sont pauvres en plancton.

c. Chaque année, la plus grande fertilité en surface s'observe durant l'hiver, et le maximum des couches moyennes (200 à 350 m.) se place en automne. Les variations plus profondes (500 à 1000 m.) sont atténuées, et assez différentes des précédentes. La décroissance quantitative suivant la profondeur est très peu accentuée, sauf en hiver.

Si les moyennes mensuelles peuvent être assez variables d'une année à l'autre, les maxima extrêmes de nanoplancton se produisent presque toujours aux mêmes dates, résultat probable des maxima de pluie et de vent, qui interviennent à des époques constantes sous le climat méditerranéen.

d. Suffisamment pourvue de lumière, la Méditerranée manque de circulation et d'échanges entre la surface et le fond, source essentielle de fertilité locale. La pluie et le vent favorisent ces mouvements de liquide et sont à l'origine des principaux changements saisonniers du nanoplancton, mais le volume annuel total de ce dernier ne paraît pas varier beaucoup, à cause de la rareté générale des phosphates qui doit être à la base de la pauvreté marine.

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(On trouvera une liste plus complète dans le mémoire No. 3 ci-dessous)

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The Hensen Net.

By

S. G. Gibbons,

Aberdeen.

IN July 1937 the question of plankton collection was discussed at Copenhagen and the sub-committee for the standardization of nets put forward a recommendation for the more general use of the Hensen net for certain types of work (1).

This net was then already in use in Scottish waters and has since been employed more frequently during the cruises of the research vessels "Explorer" and "Kathleen". The advantages of the net, *inter alia,* its low filtration coefficient under normal conditions, have already been dealt with elsewhere (2). In addition to comparisons with other types of net, however, it is thought that observations on its working under varying plankton conditions and a comparison of the results *inter se* might be interesting and useful. No plankton net yet devised is suitable for the collection of all types of organisms and the possibility that this ideal aim might be achieved by the use of a modern suction pump has been discussed (3).

It is proposed, therefore, in this short paper to consider the quantitative validity of collections made by the Hensen net. While under normal conditions there is no doubt that this apparatus gives results which are strictly quantitative, there are two factors which must be taken into account.

(1) The Size of the Organism.

It is clear that the mesh of silk used will determine the size of the organism which is retained in full numbers. When we come to organisms of slightly smaller size there is a proportion of them which must pass through the meshes, and this proportion will increase inversely as the size of the organism, until a point is reached at which none at all is retained. For quantitative work, therefore, the minimum size of animal or plant which is retained in its full numbers must be determined.

(2) Local Conditions.

In the area under consideration it is not infrequent to encounter heavy patches of certain forms which have the effect of clogging the meshes of the net. In these cases the effect is, firstly, one of diminishing the mesh of the net and so retaining smaller organisms, and, secondly, one of clogging the meshes to such an extent that filtration is badly impeded with a consequent increase in filtration coefficient. In such circumstances the quantitative value of the collection obtained is reduced to nil.

It was in order to compare the fishing of the nets in different areas that an experiment was made on the following lines.

The extent to which the meshes of the net become clogged is governed by the size of those meshes. That is to say, a standard net of fine silk will be more easily clogged than a Hensen net of coarser silk, which in its turn will be more easily clogged than a net made of coarser cheesecloth. The comparison which follows is made between a standard fine-silk net and a Hensen net. The material available was carefully examined and suitable collections for such work were found. In one case a certain area (WW20c) was sampled simultaneously by both nets to a depth of 100 metres. The fine-silk collection showed that there was a great concentration of diatoms present, mainly *Rhizosolenia* and *Chaetoceros*. Owing to the density the Hensen net contained a fair number of these species, but only partial clogging had taken place. In the fine-silk net, however, almost complete clogging must have occurred, so that poor filtration in this case would be expected. The second part of the experiment was in another area (XX17c) which, as before, was sampled simultaneously by both nets. There was no phytoplankton present, so that the best possible conditions for filtration were obtained.

The diameters of the two nets were carefully measured and the area of the opening calculated. A correction was then applied in the case of the fine-silk net to bring the numbers of animals in the collection to correspond exactly with a silk net of the same sized mouth as the Hensen net.

Comparison of Hensen and Standard Net Hauls taken at the same place and time.

Experiment 1: Heavy phytoplankton concentration.
Experiment 2: Slight phytoplankton concentration.

Experiment 1.

Hensen collection No. 38/411. Area WW20c. 60°35′N., 8°00′W. 2.7.38.
Number of *Calanus finmarchicus* (Copepodids and adults) 55,300.
Practically no phytoplankton present.
Standard collection No. 38/412. Area WW20c. 60°35′N., 8°00′W. 2.7.38.
Number of *Calanus finmarchicus* (Copepodids and adults) 1,510.
Phytoplankton abundant, with *Rhizosolenia* and *Chaetoceros* the predominating species.

Experiment 2.

Hensen collection No. 38/397. Area XX17c. 59°00′N., 6°40′W. 26.6.38.
Number of *Calanus finmarchicus* (Copepodids and adults) 5,750.
Practically no phytoplankton present.
Standard collection No. 38/396. Area XX17c. 59°00′N., 6°40′W. 26.6.38.
Number of *Calanus finmarchicus* (Copepodids and adults) 850.
Phytoplankton scarce except for several *Ceratium*.

Diameter of Hensen net opening 70 cm. Area = .379 sq.metres.
„ „ Standard „ „ 47 „ Area = .174 „ „

By multiplying the figures obtained in the case of the Standard net by $\frac{\cdot 379}{\cdot 174}$, i.e. 2·2, we obtain the number of animals which we should expect to catch with a silk net of the same sized opening as the Hensen. Any discrepancy between this figure and that taken by the Hensen net will then be due either to inferior filtration on the part of the Standard net, or to blockage of its meshes, causing it to cease functioning correctly.

From Experiment 1.

Standard: 1510 × 2·2 = 3322. Compare Hensen 55,300. Ratio 16·6.

From Experiment 2.

Standard: 850 × 2·2 = 1870. Compare Hensen 5,750. Ratio 3·1.

That is to say, that where there was a strong concentration of phytoplankton the Hensen net took more than sixteen times as many *Calanus* as did the Standard net. Where phytoplankton was scanty, however, the former net took only three times as many as the latter.

It is clear from this that where phytoplankton is abundant the filtration power of the silk net as compared with the Hensen net is very greatly impeded.

There is no doubt that for the medium-sized organisms the Hensen net under these circumstances proves its worth and is certainly the best net for quantitative examination. At the same time, however, it must not be forgotten that even the meshes of the Hensen net were, as we have seen, partially interfered with by the diatoms, so that great as is the contrast in the figures, the true state of affairs is still not fully depicted. The difference in the filtration of the Hensen net between the first and second experiment will not, of course, be so marked as the difference in the filtration in the silk-net hauls, but the fact that it is present to some extent immediately causes us to call the validity of the haul in question.

A photograph is included here of certain typical plankton organisms, upon which has been superimposed a photograph at the same magnification of pieces of material from the three types of nets commonly

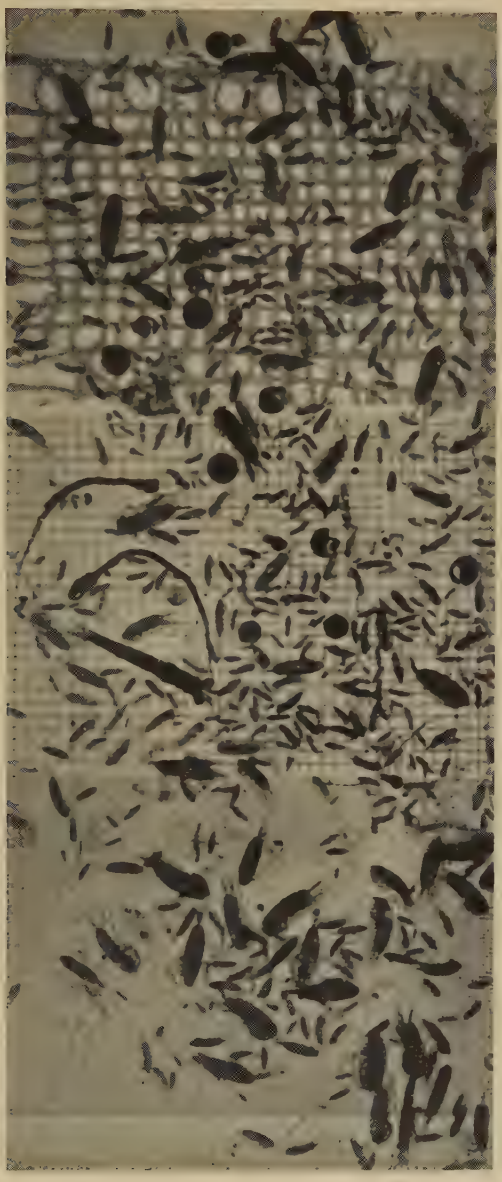

Illustration explained on page 244 (bottom) and page 246 (top).

used on our research vessels, namely, the standard fine silk, the Hensen silk and the cheesecloth. Given normal filtration conditions, it can be seen from this photograph which of the organisms are likely to be retained wholly or partially by these nets. When clogging begins to occur, it will do so first in the standard net, while the cheesecloth net on the other hand rarely, if ever, becomes clogged. I have already pointed out that the use of all three nets is necessary in studying various plankton organisms. Especially is this the case with our cheesecloth nets which procure for us samples of the larger forms such as *Sagitta,* young fish, adult *Calanus,* and so on. It is, however, more than ever apparent that comparison of the catches between the three different nets is not only impracticable but actually misleading. The increase in filtration coefficient due to clogging with the attendant decrease in the number of organisms captured will not be constant, but will probably be of a logarithmic nature. That is to say, the doubling of the filtration coefficient will result in something more than a halving of the catch. The application of a correction factor is a mathematical possibility, but it is doubtful if the result would justify the great amount of labour involved.

Unless, therefore, some means of sampling the entire plankton population from a known volume of water is practised, the problem of the planktologist becomes threefold in that he must study separately the smallest, medium-sized, and the largest plankton organisms.

The difference between the hauls of the cheesecloth nets and those taken by the Hensen net has been amply demonstrated in the plankton collections made during 1938. Throughout the year the cheesecloth nets showed that the adult *Calanus* population in Scottish waters was considerably below average. Even in the regions about Faroe, where this form usually abounds, the hauls were remarkable for their paucity of this important organism. On the other hand, however, hauls taken with the Hensen net indicated in this area particularly that quite a large population of *Calanus* was present in the early summer. The reason for this discrepancy is shown by the fact that the individuals taken in the Hensen net are practically all in young copepodid stages, hardly any of which would be retained by the cheesecloth nets. This is not the only occasion either in 1938 or in previous years upon which discrepancies of this kind have been observed. It is for this reason therefore that the planktonic sampling of any area should never be judged by the results of any one particular net. There is no doubt that for the majority of purposes the Hensen net provides the most adequate data we have. As already stated, comparisons of different nets are dangerous and it should be remembered that although the Hensen net carries with it the strongest recommendations, the results obtained from these collections should be interpreted with the greatest possible care and reserve.

It is perhaps convenient at this point to draw up a list of the common plankton organisms with notes as to their ability or otherwise to pass through the meshes of the various nets, *under normal conditions.*

Organisms Category	Fine-Silk Net	Hensen Net	Cheesecloth Net
1. Organisms larger than *Calanus*	Retained	Retained	Retained
2. *Calanus* and similar copepods	"	"	Adults retained
3. *Centropages* and *Pseudocalanus*	"	Youngest	Very few adults
4. *Temora, Acartia* etc.	"	stages	retained
5. *Paracalanus* and *Microcalanus*	"	lost	Practically all lost
6. Nauplii and small larvae	"	Mostly lost	All lost
7. Large diatoms	"	" "	" "
8. Small diatoms	"	" "	" "

It cannot be too often reiterated that in the above table we are dealing with filtration under normal conditions — that is to say, we are allowing for no clogging in any of the nets. If such clogging occurs, the size of organism retained will be diminished in each case, and this is why we find on occasion some of even the smallest organisms such as calanoid nauplii retained by the largest meshed nets.

In the first category in the above table we should normally include all the large copepods such as *Euchaeta* and *Calanus hyperboreus,* all the copepodid stages of which will also be retained by the Hensen net. Decapod larvae of many varieties, Schizopods, the Sagittas, small and large Medusae, *Oikopleura,* as well as most fish eggs and all the pelagic fish larvae will also fall into this group. In Categories 2 to 5, we find an increasing number of escapes in the two coarser nets as size diminishes. Except in cases of reduced filtration as outlined above, nauplii will in general be retained only by the fine-silk net.

The true individual distribution of organisms in the sea does not seem to be sufficiently realized. When several thousand copepodids of *Calanus* are taken in the Hensen net, for example, one is apt to regard the form as fairly abundant, as indeed it is. Nevertheless, if one bears in mind the huge quantity of water which has been filtered by the net, it is seen that the distribution becomes of the order of one *Calanus* per litre; and even one per ten litres would not be considered really scanty distribution, if one studied the collection as a whole. It will be clear, therefore, that true quantitative work demands the filtration of as large a volume of water a possible, and for this reason it is considered that the small diameter pumps as used by early workers were inadequate. A large diameter high delivery pump is essential, and even then it is not suggested that it should entirely replace nets, especially for qualitative work.

In conclusion, a word as to the method of working the Hensen net may be added. Although no spring accumulator was used on the "Explorer", the recognized speed of hauling at ½ m. per second was observed in all cases and adhered to as far as possible. In order to compensate for the rolling of the ship in heavy weather the method of counterweight and pulley was used in several of the hauls. The difficulty of broadside drift due to wind resistance on the ship is, however, always present. In these cases, as with other vertical nets, the angle at which the net comes back to the ship is sometimes as much as 45° so that the haul is far from vertical, and since the maximum

amount of drag occurs in the last stages of the haul, it is likewise not strictly oblique.

The conclusion reached, therefore, with regard to the Hensen net is that it is the best general-purpose net in use to-day. It is not devoid of the usual disadvantages incumbent upon all plankton net work, but it represents great development in the reduction of error to a minimum. At the same time, the results obtained by it must be interpreted with the greatest care.

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Der Atmungsmechanismus der Teleosteer.

Von

J. Henschel,
Helgoland.

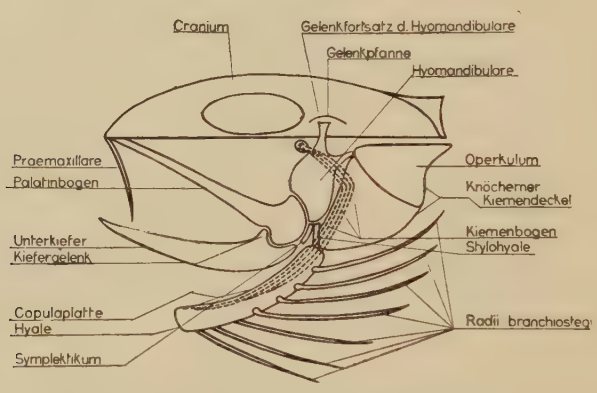
Einleitung.

DIE Atmungsbewegungen der Fische haben schon frühzeitig naturwissenschaftliche Forscher zu Beobachtungen angeregt. Bereits im 18. Jahrhundert machte man sich Gedanken darüber, welcher Mechanismus wohl den Fischen mit ihren rhythmischen Atmungsbewegungen zur Verfügung stehen könnte, um dauernd einen Strom von frischem Wasser an ihren Kiemen vorbeizuführen. Die französischen Forscher Duverney und besonders Dumeril und Flourens hielten die Atmungsbewegung für eine Art Schluckbewegung (nach Babák (1)). Der Fisch sollte danach Wasser schlucken, wie er ein Beutestück schluckt. Durch peristaltische Bewegungen, Zusammenpressen erst der Mundhöhle, dann der Kiemenhöhlen sollte das Wasser langsam nach hinten zu den Kiemenspalten geleitet werden. Später erkannte man, dass es sich bei den Atmungsbewegungen um Pumpbewegungen handelt. Besonders hervorgehoben werden müssen hier die Beobachtungen von Baglioni (2), der den Pumpmechanismus des Branchiovisceralapparats entdeckte. Er entwarf ein Schema dieser komplizierten Bewegungen, das viel richtige Einzelheiten enthielt und auch lange Zeit für die befriedigendste Erklärung gehalten wurde. In neuester Zeit hat Woskoboinikoff (6) auf Grund von anatomischen Studien des Visceralskeletts allerdings feststellen müssen, dass die Bewegungen doch in wesentlichen Punkten von Baglionis Schema abwichen und dass der Atmungsvorgang komplizierter ist, als es sich Baglioni vorgestellt hatte. Seine Arbeiten haben der Forschung auf diesem Gebiet neue Anregungen gegeben.

Der Bauplan des Branchiovisceralapparats.

Das Respirationsorgan, an welchem dauernd frisches Wasser zur Sauerstoffaufnahme vorbeigeführt werden soll, sind die Kiemen. Jede Kieme besteht bekanntlich aus einem Kiemenbogen, auf dem in zwei Reihen angeordnet die Kiemenblättchen stehen. Jede Blättchenreihe

bildet eine Halbkieme. Die Blättchen sind in Septen angeordnet. Sie stehen auf dem konvexen Rande der Kiemenbögen, ragen also nach hinten in die seitliche Kiemenhöhle. Jedes Blättchen besitzt als Stütze eine Skelettlamelle, die im Bindegewebe des Bogens verankert ist. Diese Lamelle fixiert die Stellung der Blättchen, die etwas nach aussen geneigt sind. Die Skelettlamellen werden von der respiratorischen Membran überzogen, die über den Breitseiten der Lamellen erhabene Leisten bildet, die sog. sekundären Blättchen. Zwischen den Halbkiemen laufen die zu- und abführenden Gefässe. Gekreuzte Muskeln verengen und erweitern diese, sie spielen also die Rolle von Kiemenherzen.



Der Bauplan des Kabeljauschädels (schematisch).

Der Fisch[1]) besitzt bekanntlich 4 Kiemenbogenpaare. Sie sind jederseits der Mittellinie im Bindegewebe der Schädelbasis — anders ausgedrückt des Munddachs — verankert. Sie senken sich, je 4 Einzelbögen nebeneinander, in einem etwas nach aussen geschwungenen Bogen zum Mundboden und laufen an den seitlichen Zonen des Mundbodens nach vorn. Zwischen den Bögen des innersten Paares ist die vom Oesophagus durchbohrte Schlundwand ausgespannt. Die Einzelbögen jeder Seite stossen hinter dem Zungenhügel, ein Paar hinter dem anderen, in der ventralen Mittellinie des Mundbodens zusammen. Die Verbindungsknochen der Bögen bilden dort einen festen Knochensteg, die Copulaplatte, die sich bis zur hinteren Schlundwand erstreckt.

Vor den Kiemenbögen liegt die unpaare Mundhöhle. Durch die Spalten zwischen den Kiemenbögen gelangt man in die paarigen, lateralen Kiemenhöhlen. Sie liegen demnach seitlich hinter den Kiemenbögen und zugleich seitlich des vorderen Rumpfendes, das sich unter den Mundboden keilförmig vorschiebt; auf die Mundhöhle bezogen, hinter ihr, im ventralen Bezirk, auch unter derselben. Beide Kiemenhöhlen stossen im ventralen Bezirk zusammen. Sie sind überdeckt vom

[1]) Als Vorbild für die Beschreibung hat der Schädel von *Gadus* gedient.

Kiemendeckel und münden durch den Kiemenspalt zwischen Kiemendeckel und Schultergürtel nach aussen.

Um den Mechanismus der komplizierten Bewegungen zu verstehen, muss man sich den Bauplan dieser Bewegungsapparatur noch genauer betrachten. (Siehe Abbildung.) Das Gerüst für Mund- und Kiemenhöhlen liefert das Visceralskelett. Es besteht aus einer Anzahl Knochenbögen. Der 1. Bogen, der Kieferbogen besteht aus einer Knochenplatte, die nach vorn in eine Knochenstrebe ausläuft und bis in die Nasenregion des Schädels reicht. Sie ist aus einer Reihe von Knochen zusammengesetzt: dem Quadratum, den Pterygoiden und dem Palatinum. Am Quadratum, mit dieser Knochenplatte durch das Kiefergelenk verbunden, ist die ventrale Spange dieses Bogens, der Unterkiefer. Der Oberkiefer wird nicht von einem Knochenstück des Kieferbogens gebildet, sondern von einem neu hinzutretenden Knochen, dem Praemaxillare.

Die folgenden Bögen, der 2. bis 7. Bogen, haben einen einander ähnlichen Verlauf. Sie besitzen kürzere dorsale Glieder, die vom Cranium ausgehend sich nach hinten und etwas nach aussen senken. Ihre ventralen Stücke sind länger. Sie sind gegen die dorsalen eingeknickt, senken sich nach innen und vorn und stossen in der ventralen Mittellinie zusammen.

Der 2. Bogen ist der *Hyoid-* oder *Zungenbeinbogen.* Sein dorsales Glied ist das Hyomandibulare, eine unregelmässig geformte Knochenplatte mit vorspringenden Leisten zum Muskelansatz. Mit einem Gelenkfortsatz ist es mit dem Schädel verbunden. Der Gelenkfortsatz ruht in einer Gelenkpfanne, die sich in der Occipitalregion des Schädels befindet. Das Hyomandibulare ist mit dem Kieferbogen und zwar mit dem Metapterygoid fest verwachsen, während sich ein ihm anhängender kleiner Knochenstab, das Symplektikum, mit dem Quadratum verbindet. Das Hyomandibulare wird daher zum Verbindungsglied zwischen Kieferbogen und Cranium. Man bezeichnet diese Knochenanordnung bekanntlich als H y o s t y l i e des Schädels. Sie tritt nur bei Fischen auf und steht zum Atmungsmechanismus in funktioneller Beziehung, weswegen die Verhältnisse auch so genau beschrieben werden müssen. Der ventrale Teil dieses Bogens, das Hyale oder Zungenbein, ist mit dem Hyomandibulare nicht direkt, sondern durch einen kleinen Knochenstab, das Stylohyale, verbunden. Das Zungenbein selbst ist eine breite Knochenleiste, die sich von der Seitenregion des visceralen Schädels nach unten zur ventralen Mittellinie des Mundbodens senkt und sich dort mit dem Zungenbein der anderen Seite verbindet.

Die nächsten Bögen, die *4 Kiemenbögen,* sind nach innen gerückt. Über ihren Verlauf wurde schon gesprochen. Sie setzen sich ebenfalls aus kurzen dorsalen und längeren ventralen Gliedern zusammen, die sich in der ventralen Mittellinie des Mundbodens hinter dem Hyoidbogen paarweise treffen. Sie sind dort durch Verbindungsglieder, die Copula, miteinander und mit dem Hyoidbogen verwachsen und bilden eine feste Knochenbrücke, die bereits erwähnte Copulaplatte.

Der 5. Kiemenbogen ist rückgebildet. Es sind von ihm nur die ventralen Stücke übriggeblieben, die die Schlundzähne des Mundbodens tragen.

Von aussen werden die Kiemenbögen bekanntlich verdeckt und geschützt von den Kiemendeckeln, die am Hyoidbogen befestigt sind. Wie jener besteht jeder Kiemendeckel aus einem dorsalen Teil, dem *knöchernen,* dem eigentlichen *Kiemendeckel,* und einem ventralen Teil, der *Branchiostegalmembran* oder *Kiemendeckelhaut.* Der knöcherne Kiemendeckel ist mit dem Hyomandibulare verbunden; er sitzt an einem Gelenkfortsatz dieses Knochens, sodass er auch eigene Bewegungen ausführen kann. Er besteht aus den Operculaknochen, 4 Knochenplatten, von denen aber eine zum Quadratum und den Pterygoiden in nähere Beziehungen getreten ist. Der ventrale Teil, die Branchiostegalmembran, ist mit dem Hyale verwachsen. Sie ist eine derbe Haut, die durch 7 elastische, nach oben und auswärts gewölbte Knochenstäbe, die *Radii branchiostegi,* versteift wird. Diese Knochenstrahlen sind am Hyale befestigt und enden frei in der Membran. Die Membranen beider Seiten gehen im ventralen Bezirk unter dem Rumpfkeil, den sie hülsenförmig umschliessen, ineinander über.

In die Betrachtung des Skeletts müssen noch die Knochen des *sekundären Schultergürtels* einbezogen werden. Die Cleitra bilden die Stützen des sich unter den Mundboden auskeilenden Rumpfabschnitts. Sie beginnen in der Region der ersten Wirbel, verlaufen nach vorn und unten und treffen sich von jeder Rumpfseite kommend unter dem Mundboden, genauer unter dem hinteren Abschnitt der Copulaplatte.

Die Bewegungen des Branchiovisceralapparats.

An diesen Skeletteilen lässt sich der Bewegungsmechanismus des Branchiovisceralapparats klarmachen. Wenn man einen Fisch im Aquarium beobachtet, bemerkt man, dass er Mund- und Kiemenhöhle im Atmungsrhythmus erweitert und verengt. Die Erweiterung findet in zwei Richtungen statt: Einmal in der dorsoventralen Achse nach unten, zweitens nach den Seiten durch Abspreizen der Backenpartie. Wie kommen diese Bewegungen zustande? Ein starker Muskel, der vom Zungenbeinbogen unter der Copulaplatte zum Schultergürtel führt, der *Musculus sternohyoideus,* zieht den Zungenbeinbogen und mit ihm den Unterkiefer hinab. Er öffnet das Maul und erweitert die Mundhöhle in ventraler Richtung. Seine Antagonisten sind der *Musculus adductor mandibularis,* der den Unterkiefer anzieht und das Maul schliesst und der *Musculus geniohyoideus,* der den Zungenbeinbogen nach oben zieht und die Mundhöhle verengt. (Der Adductor mandibularis bildet die starke Muskelmasse der Backenregion. Der Geniohyoideus zieht in der Kehlhaut vom Unterkiefer zur Aussenseite des Hyale.)

Bei der Atmung führt der Unterkiefer meist nur geringe Bewegungen aus, während der Zungenbeinbogen in der Kehlhaut kräftig hin und

herwandert und sie auswölbt. Dies ist dadurch möglich, dass der Unterkiefer durch bestimmte Fasern des Add. mand. fixiert gehalten wird. Mit dem Zungenbeinbogen werden auch die Kiemenbögen hinabgezogen, da sie ja mit ihm verbunden sind.

Offenbar ist es für das Tier wichtig, die Mundhöhle zu erweitern, ohne den Durchmesser der Mundöffnung zu vergrössern, weil dadurch die Saugkraft auf das einströmende Wasser erhöht wird. Ausserdem mag es für im Sande vergraben lebende Fische noch eine besondere Bedeutung haben. Unterkieferbewegungen würden den Sand stark aufwirbeln, was von dem Tier wohl vermieden werden soll.

Das Ziel wird in noch stärkerem Masse durch die seitliche Erweiterung der Mundhöhle erreicht. Diese kann bereits passiv durch Senken des Zungenbeinbogens zustande kommen. Weil das Hyale dorsal keinen festen Drehpunkt besitzt, drückt sein dorsales Ende beim Zurückgezogenwerden gegen das Hyomandibulare. Dieses kann aber nicht nach oben ausweichen, weil es dorsal am Schädel festgewachsen ist. Es bleibt der Knochenkette des Zungenbeinbogens nun nichts weiter übrig, als nach aussen abzuknicken. Diese Bewegung wird durch das Einschalten des Stylohyale als Zwischenknochen noch erleichtert und vergrössert.

Mit dem Hyomandibulare hebt sich aber die ganze Knochenplatte der Backenpartie ab, da ja alle Knochen mit ihm in Verbindung stehen: Der Palatinbogen, Quadratplatte, Kiemendeckel. Man erkennt die Bedeutung des hyostylen Schädels für den Bewegungsmechanismus. Alle Knochen sind auf einen Drehpunkt bezogen und so kann ein einziger Muskel das ganze Hebelsystem bedienen. Andererseits wird die seitliche Abhebung und Adduction auch aktiv durch eine Reihe von Muskeln bewerkstelligt, die die dorsalen Bogenglieder bedienen: Die *Levatoren, Dilatatoren* und *Adductoren* der Palatinbögen, des Hyomandibulare und des Operculum. Diese Muskeln liegen teilweise unter der Muskelmasse des Adductor mandibularis, teilweise über dem Munddach, schliesslich neben der Occipitalregion des Schädels. Auch sie setzen in umgekehrter Reihenfolge die ganze Hebelkette in Bewegung. Man erkennt wieder die Bedeutung des hyostylen Schädels. Natürlich erleichtert die Hyostylie auch das Verschlingen grosser Beutestücke. Sie dient den beiden Funktionen des Visceralskeletts, Nahrungsaufnahme und Atmung gleichzeitig.

Die Funktion von Mund- und Kiemenhöhle.

Was geschieht durch diese rhythmische Erweiterung und Verengung von Mund- und Kiemenhöhle? Betrachten wir zunächst beide Höhlen getrennt voneinander. Die Erweiterung entspricht der Inspiration. Durch den nur wenig geöffneten Mund wird in den erweiterten Mundhohlraum Wasser gesaugt, das in der Exspiration durch Verengung der Höhle an den Kiemen vorbei durch die Kiemenspalten wieder ausgestossen wird. Die Saugwirkung der Mundhöhle wird umso grösser, je weniger das Maul dabei geöffnet wird. Manche Fische haben daher

ganz auf die Unterkieferbewegungen verzichtet. Den Rückstrom des Wassers in der Exspiration verhindert das Spiel der Mundklappen, die als Rückschlagventil fungieren. Die Mundklappen sind Hautfalten, die zwischen Ober- bzw. Unterkiefer ausgespannt sind. In der Inspiration werden sie vom eindringenden Wasser in die Mundhöhle zurückgeschlagen, in der Exspiration aber werden sie vom Rückstrom des Wassers vor die Mundöffnung gedrückt, aneinander gepresst und verwehren dem Wasser den Durchtritt durch die Mundöffnung, sodass es nach hinten ausgepresst werden muss. Trotz der geringen Saugkraft, die auch die Mundhöhle bei ihrer Erweiterung entwickeln kann, muss man in ihren Druckkräften, die sie durch Verengung in der Exspiration entwickelt, die grössere Arbeitsleistung erblicken, sodass ihr Mechanismus wohl mit der Arbeit einer Druckpumpe verglichen werden kann.

Dagegen entspricht die Arbeit der seitlichen Kiemenhöhlen der Wirkung zweier Saugpumpen. Diese sind nämlich durch die Wände der Kiemenblättchen von der Mundhöhle vollkommen getrennt. Die Trennung kommt durch die charakteristische Stellung der Kiemenblättchen zustande. Sie hängen nicht schlaff nach hinten in die seitlichen Kiemenhöhlen, sondern die Blättchen jeder Halbkieme neigen sich der Halbkieme des ihnen benachbarten Bogens zu. Hierbei berühren sich ihre Spitzen. Weil nun die Blättchen jeder Halbkieme durch die sekundären Blättchen miteinander verzahnt sind, bildet die gesamte Kiemenblattfläche eine kompakte Gitterwand. Dies hat einmal eine sehr grosse Sauerstoffausnutzung des durchströmenden Wassers zur Folge. Die Gitterwand bekommt aber auch für den Atmungsmechanismus der Kiemenhöhlen Bedeutung. In der Inspirationsphase erweitern sich auch die seitlichen Kiemenhöhlen durch Abhebung der Kiemendeckel und Auswölbung der Branchiostegalmembran. Der Wasserdurchtritt aus der Mundhöhle in die Kiemenhöhlen wird aber durch das Blättchengitter verzögert. Dadurch entsteht in den Kiemenhöhlen ein Unterdruck, der mit erheblicher Saugkraft das Wasser aus der Mundhöhle durch das Kiemenblattgitter in die seitlichen Kiemenhöhlen saugt. Voraussetzung dafür ist allerdings, dass die Kiemenspalten vom Kiemendeckel und von der Branchiostegalmembran fest verschlossen werden. Dies ist tatsächlich der Fall. Der weiche Hautrand des Kiemendeckels und der Saum der Kiemendeckelhaut werden durch den äusseren Wasserdruck gegen den Schultergürtel gepresst, sodass sie den Spalt verschliessen. Ausserdem werden die distalen Ränder der Kiemendeckelapparatur auch durch Muskeln an den Schultergürtel angelegt, während sich ihre proximalen Teile abduzieren. Der Schultergürtel selbst ist in die laterale Kiemenhöhle geneigt und hat eine schmale Gleitfläche ausgebildet, die sich der Bewegungsweise der Branchiostegalmembran gut anpasst, wenn sie durch die Hyalia nach hinten geschoben und wieder nach vorn zurückgezogen wird. Auf jeden Fall verschliesst also der Kiemendeckelapparat den Kiemenspalt vollständig, sodass sich der Unterdruck in den lateralen Kiemenhöhlen entwickeln kann.

Im Bau des Kiemendeckelapparats lassen sich noch weitere Einzelheiten entdecken, die eine Anpassung an die Pumpfunktion darstellen.

Die Knochenwand des eigentlichen Kiemendeckels ist besonders dafür geeignet, die Kiemenhöhle gegen den äusseren Wasserdruck zu erweitern. Dagegen hat die Branchiostegalmembran die Funktion, sich dem Fischkörper eng anzulegen, dort, wo er aus der Seitenfläche in die Bauchfläche übergeht. Dazu ist sie durch ihre Schmiegsamkeit und durch die Form ihrer nach aussen gewölbten Knochenstrahlen besonders geeignet. Wenn man sich die Ansatzstellen der 7 Strahlen am Hyale genauer betrachtet, bemerkt man, dass die ersten 3 Strahlen, die die Bauchfläche bestreichen, an der Innenfläche der Hyalia festgewachsen sind, wodurch sie sich ihr besser anlegen können. Die 4 letzten sind dagegen aussen angewachsen. Sie bestreichen die Seitenfläche des Rumpfs, der sich etwas gegen den Umriss des Kopfes vorwölbt.

In der Exspiration heben sich Kiemendeckel und Branchiostegalmembran vom Schultergürtel ab, die Kiemenhöhlen werden verengt und das verbrauchte Wasser durch die Kiemenspalten ausgestossen.

Experimente.

Die verschiedenen Kräfte, die bei der Pumparbeit entwickelt werden, lassen sich experimentell nachweisen. Ich habe an der Biologischen Anstalt von Helgoland eine Reihe solcher Versuche ausführen können. Für Versuche eignen sich besonders Bodenfische, die sich auch in den Versuchsgefässen im grossen und ganzen ruhig verhalten.

Wenn man z. B. einer Scholle den äusseren Rand der Branchiostegalmembran abschneidet, nimmt man ihr die Funktion der lateralen Kiemenhöhlen. Sie ist nun auf die Arbeit der Mundhöhle allein angewiesen. Was tut sie? Sie steigert die Atemfrequenz. (Ich beobachtete im Durchschnitt eine Steigerung von 46 auf 67 Atemzügen pro Minute.) Sie erweitert die Mundhöhle stärker als normal, besonders in ventraler Richtung. In die Bewegungen wird der Unterkiefer mit einbezogen, der heftig auf und zuklappt. Das Tier, dem ja der Saugpumpenmechanismus der lateralen Kiemenhöhlen genommen ist, verzichtet nun ganz auf die Wirkung der Saugkräfte und stellt sich auf die alleinige Arbeit der Druckpumpe ein. Die Bewegungen sind beschleunigt und heftig, ihre Hauptkraft entfaltet die Mundhöhle in der auch normalerweise sehr kurzen Exspirationsphase, in der die Atmungsapparatur die Arbeit einer Druckpumpe leistet. Der Sauerstoffverbrauch hält sich dabei in normalen Grenzen. Das Tier ist also imstande, auch durch Arbeit der Mundhöhle allein seinem Blut den nötigen Sauerstoff zuzuführen.

Umgekehrt, wenn man dem Fisch ein kleines Rohr im Maul befestigt, muss er auf die Arbeit der Mundhöhle verzichten, weil er ja den Rückstrom des Wassers in der Exspiration nicht mehr verhindern kann. Jetzt verlangsamt er die Atemfrequenz (im Durchschnitt von 46 auf 36 Atemzüge pro Minute). Hierbei wölbte sich die Branchiostegalmembran stärker nach hinten aus als normal, während Palatinbogen und Hyale häufig fixiert gehalten werden. In dieser Lage wird also die Saugperiode verlängert, die Saugkraft durch stärkere Erweiterung

der lateralen Kiemenhöhlen erhöht. Die lateralen Kiemenhöhlen spielen in der langsameren Inspirationsphase die Hauptrolle, sie arbeiten als Saugpumpen. Der Sauerstoffverbrauch hielt sich auch bei dieser Arbeitsweise in normalen Grenzen.

Es muss interessieren, welche Saugkräfte die lateralen Kiemenhöhlen überhaupt entwickeln können. Ich liess zu diesem Zweck auf Backsteinen gefesselte Plattfische aus einem Zylinder Wasser saugen. Die Anordnung war folgendermassen: Die gefesselten Tiere wurden in ein Aquarium gesetzt. Eine Schlauchleitung, die im Maule des Tieres wasserdicht befestigt war, führte in den neben dem Aquarium aufgestellen Standzylinder, der ebenso wie das Aquarium mit Seewasser gefüllt war. Die Wasserspiegel beider Gefässe waren anfangs auf gleiches Niveau gestellt. Mit jedem Atemzug des Fisches erniedrigte sich aber der Wasserspiegel im Standzylinder. Der Fisch musste also gegen das hydrostatische Gefälle Wasser saugen. Damit das Wasser während der Exspirationsphase nicht zurückströmte, wurde ein Rückschlagventil in die Schlauchleitung eingeschaltet, das die Mundklappen ersetzte. Eine über 20 cm. lange Scholle konnte bis 2·8 cm. Niveau-Unterschied Wasser saugen.

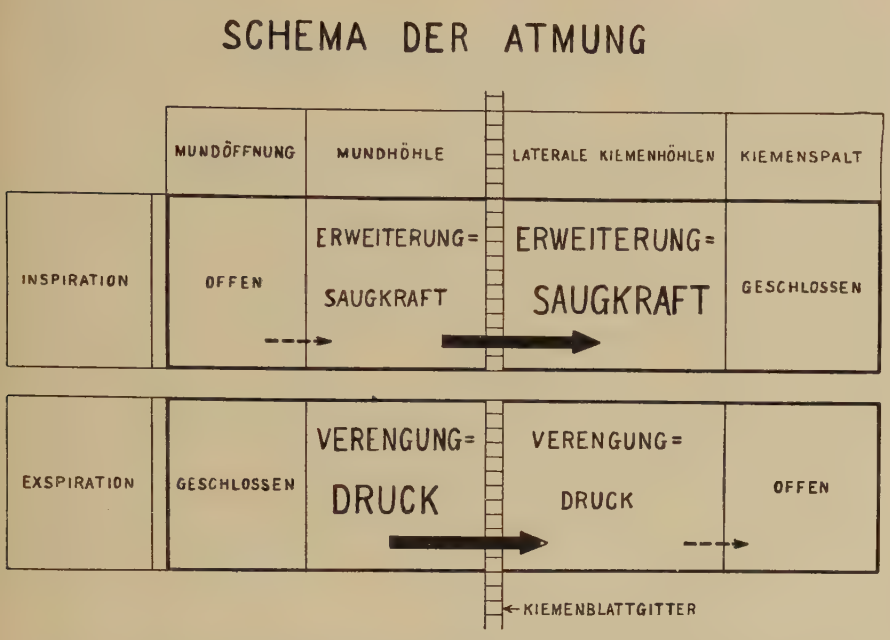
Weiter wurden Fische vor ein schlangenförmig gebogenes Glasrohr gespannt, das horizontal ins Wasserbecken gelegt werden konnte. Hier brauchte der Fisch also nicht gegen das hydrostatische Gefälle zu saugen. An der Wanderung einer Luftblase konnte man die Wassermenge abmessen, die er mit jedem Atemzug ansaugt. Das sind für eine etwa 20 cm. Scholle 0·5 bis 0·6 c.c. Der Reibungswiderstand ist bei dieser Apparatur recht gross, die Atemzüge waren dementsprechend verlangsamt. Stärker als normal trat auch die Atmung der Branchiostegalmembran in den Vordergrund.

Wenn man den Tieren den äusseren Rand der Branchiostegalmembran abschnitt, konnten sie überhaupt nicht mehr unter den Versuchsbedingungen Wasser saugen, ein Beweis dafür, dass die lateralen Kiemenhöhlen wirklich grosse Saugkräfte entwickeln.

Diese Versuche, zwar nicht unter normalen Bedingungen ausgeführt, zeigen uns aber doch das Prinzip, nach dem die Hohlräume der Atmungsapparatur arbeiten, und wir können uns nun die Arbeit eines Fisches bei normaler Atmung rekonstruieren.

Die Inspiration: Die Mundhöhle wird erweitert und füllt sich mit Wasser. Mit der Mundhöhle erweitern sich auch die lateralen Kiemenhöhlen, die mit recht erheblichen Kräften das Wasser durch das Kiemenblattgitter in ihre Hohlräume saugen. Sie leisten die Hauptarbeit in dieser Phase, die Saugwirkung der Mundhöhle tritt ihnen gegenüber in den Hintergrund.

Die maximale Erweiterung ist erreicht. Es tritt die Exspiration ein. Die Kiemenspalten, bisher geschlossen, öffnen sich, Mundhöhle und seitliche Kiemenhöhle pressen sich zusammen, der Mundspalt wird geschlossen, das Wasser nach hinten ausgepresst. Die Mundhöhle, die das Wasser durch das Kiemenblattgitter zu pressen hat, leistet in dieser Phase die Hauptarbeit. Ein Schema soll das verdeutlichen. Man



erkennt, dass jeweils diejenige Höhle die grössere Pumparbeit leistet, die das Wasser durch die Gitterwand der Kiemenblättchen zu transportieren hat, die Kiemenhöhlen als Saugpumpen, die Mundhöhle als Druckpumpe.

Ohne Pause also, in der Inspiration und in der Exspiration wird sauerstoffreiches Wasser an den Kiemen vorbeigeführt, sodass der Fisch ohne Unterbrechung atmen kann. Dazu verhilft ihm diese überaus komplizierte Apparatur, die er im Zusammenspiel von Mund- und Kiemenhöhle besitzt.

Abänderungen des normalen Typus.

Die verschiedenen Lebensweisen haben die Atmungsapparatur nach verschiedenen Seiten hin abgeändert. Normale Verhältnisse finden wir z. B. beim Kabeljau. Der Kabeljau schwimmt viel umher und gelangt häufig in frisches, sauerstoffreiches Wasser. Gelegentlich hält er sich aber auch längere Zeit an ein- und derselben Stelle auf, wobei die Wassererneuerung hauptsächlich von seinen Atmungsbewegungen besorgt werden muss. Bei ihm sind alle Glieder der Atmungsapparatur gleichmässig entwickelt.

Abänderungen haben einmal Fische erlitten, die eine stillsitzende Lebensweise führen und sich vorwiegend am Boden aufhalten. Für sie ist es wichtig, dass sie mit dem Exspirationsstrom nicht den Schlick oder feinen Sand, auf dem sie leben, aufwühlen. Sie leiten das Wasser durch eine eng umgrenzte Exspirationsöffnung nach aussen, die am

dorsalen Rand des Kiemendeckels gelegen ist. Nehmen wir als Beispiel *Trigla.* Der knöcherne Kiemendeckel biegt am hinteren dorsalen Rande nach vorn um und buchtet sich aus. Es entsteht eine elliptische Öffnung, über die der weiche Rand des Kiemendeckels zu einer Hautklappe, der sogenannten Branchiostegalklappe, ausgewachsen ist. Sie spielt im Atmungsrhythmus wie ein Klappenventil. In der Inspiration wird sie durch den äusseren Wasserdruck gegen die Schädelwand gepresst und schliesst die Öffnung. In der Exspiration hebt sie sich durch den Wasserdruck von innen ab. Dagegen hebt sich die Branchiostegalmembran auch in der Exspirationsphase nicht vom Schultergürtel ab, der Kiemenspalt bleibt also dauernd geschlossen. Der Exspirationsstrom wird nach oben durch die Klappenöffnung ausgestossen.

Tiere, die im Sand vergraben leben, z. B. Plattfische, haben weitere Abänderungen erfahren. Für sie kommt es darauf an, auch während der Inspirationsphase einen möglichst intensiven Wasserstrom zu erzeugen. Denn sie gelangen ja lange Zeit nicht in sauerstoffreiches Wasser, sondern müssen sich dieses herbeischaffen. Dementsprechend ist die Saugkraft ihrer seitlichen Kiemenhöhlen vergrössert. Mehr als bei anderen Fischen tritt die Tätigkeit der Branchiostegalmembran in den Vordergrund, die sich nach hinten über den Schultergürtel ausspannt und die Kiemenhöhle auch in dieser Richtung erweitert. Ihre Bewegung leitet gleichzeitig das Atemwasser zur Exspirationsklappe, die diese Tiere natürlich auch besitzen. Bei Plattfischen wird selbst die Klappenöffnung nicht passiv durch den Druck des Wassers, sondern aktiv durch Muskeltätigkeit geöffnet und geschlossen. Ein sehr kompliziertes Muskelsystem, das die Kiemenhautstrahlen bedient, spannt dieselben während der Inspiration fächerförmig aus und zieht sie während der Exspiration wieder zurück. Der 7. Strahl, der, wie alle, nach oben gebogen ist, reicht bis in den äusseren Rand der Branchiostegalklappe und zieht diese selbst entsprechend seiner Bewegungsweise vor und zurück. Haben Plattfische neben der Tätigkeit der Branchiostegalmembran auch noch alle anderen Glieder des Apparats voll entwickelt und in Funktion, so stellt *Trachinus* einen Extremfall dar. Er atmet allein mit der Branchiostegalmembran.

Eine andere Entwicklungsmöglichkeit war gegeben bei Dauerschwimmern. Diese Tiere brauchen ja nicht so starke Atembewegungen auszuführen wie trägere Tiere, weil sie ständig durch ihren Ortswechsel in sauerstoffreiches Wasser gelangen. Wir sehen bei ihnen auch die Atmungsapparatur mehr oder weniger rückgebildet. Einen Extremfall dieser Gruppe stellt die Makrele dar. Sie hat auf Atmungsbewegungen fast ganz verzichtet. Ihr Branchiovisceralapparat ist so entwickelt, dass er ein möglichst schnelles Durchstreichen des Wassers, das diese schnellen Schwimmer durchschiessen, gestattet. Sie kann die Mundöffnung nicht vollkommen schliessen. Ihre Branchiostegalmembran ist in der Kehlregion tief eingeschnitten, sodass auch die seitlichen Kiemenhöhlen nicht mehr fest verschlossen werden können. Die Kiemenblätter bilden kein kompaktes Gitter, sondern stehen in weitem

Abstand voneinander auf den Bögen. Sie sind steif und borstenförmig. Alles Einrichtungen, die ein hemmungsloses Vorbeistreichen des Wassers erleichtern. Eine gefesselte Makrele kann dagegen ihr Blut nicht mehr mit Sauerstoff sättigen.

Es gibt andere Abänderungen, die nicht aus der Lebensweise der Tiere zu erklären sind, sondern rein morphologische Differenzierungen vorstellen. Die auffälligste ist der Wegfall der Branchiostegalstrahlen, der bei einer Reihe von Fischen stattgefunden hat. Diese Fische besitzen dann oft eine derbe Haut, die mit der Körperwand weitgehend verwachsen ist und nur eine schmale Kiemenspaltöffnung zum Austritt des Atemwassers offen gelassen hat. Die Erweiterung der lateralen Kiemenhöhlen besorgt der knöcherne Kiemendeckel, der in die derbe Haut eingelagert ist. Als Beispiele sind zu nennen *Lophus* und weiter *Conger*, der Seeaal, während der Flussaal Kiemenhautstrahlen besitzt.

Im einzelnen weisen Form und Funktion der verschiedenen Fischarten noch mancherlei Unterschiede auf, die hier nicht mehr angeführt werden können und wohl auch zum grossen Teil noch garnicht genau untersucht worden sind, sodass sich hier noch ein breites Beobachtungsfeld für den Forscher bietet.

Summary.

The problem discussed is, What mechanical force is used by a fish to secure a continuous flow of water past the gills for obtaining oxygen? To illustrate the complicated action producing the flow of respirative water the construction of the branchiovisceral skeleton is described and the physiology of the respiratory movements is explained on the basis of the work of modern and older authors as well as of the author's experiments.

In the closed mouth-gill cavity formed by the branchiovisceral skeleton three separate cavities can be distinguished, namely, the mouth cavity and the two lateral gill cavities, the latter being separated from the mouth cavity by the branchiostegal rays. The fish produces a continuous flow of water from the mouth into the mouth cavity and through the branchiostegal rays into the lateral gill cavities and finally out into the water through the gill clefts. The mouth cavity acts chiefly as a pressure pump: during exhalation, water drawn in during inhalation is pressed into the lateral gill cavities. The lateral gill cavities act as suction pumps: during inhalation water is drawn with considerable force from the mouth cavity. The pump action is performed simultaneously with a rhythmical extension and contraction of the mouth cavity. Extension and contraction occur in two directions, viz., dorso-ventral and lateral. The lateral extension stimulates the suction movement. The dorso-ventral action mainly serves as the pressure pump mechanism of the mouth cavity. The uniformity of the complicated action is chiefly dependent upon the hyoid bones. The arrangement of these bones further permits of a strong lateral extension of the cavities thus intensifying their suction force considerably.

Finally, various modifications in the normal types of respiration in various species are described.

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Untersuchungen an Jungflundern (*Pleuronectes flesus* L.) der Samlandküste.

Von

Günther Hass,

Seefischereistation Neukuhren des Fischerei-Instituts
der Universität Königsberg i. Pr.

I.

DIE Flundernfischerei ist für die Seefischerei Ostpreussens von grösster wirtschaftlicher Bedeutung. Die Strandfischer, welche die Fischerei von offenen Motorbooten aus mit Stellnetzen nur in der Nähe der Küste betreiben, fangen während der Sommermonate ausschliesslich Flundern; aber auch die Kutterflotte geht während des grössten Teiles des Jahres auf Flundernfang und zwar sogleich nach Beendigung der gesetzlichen Schonzeit bis in den Dezember hinein. Lediglich in den beiden ersten Monaten des Jahres werden von den ostpreussischen Seefischern keine Flundern gefangen.

Tabelle 1.

Jahr	Flundern in kg.
1930	368,959
1931	255,260
1932	493,135
1933	322,100
1934	517,245
1935	755,310
1936	1,137,000
1937	1,100,730

Tabelle 2.

Jahr	Flundern in kg.
1930	9,527
1931	16,834
1932	80,289
1933	114,174
1934	115,000
1935	182,553
1936	291,268
1937	378,596

Tabelle 1 zeigt die Gesamtmengen an Flundern, die in den Jahren 1930 bis 1937 in allen ostpreussischen Fischereihäfen gelandet wurden und Tabelle 2 die allein von der Neukuhrener Kutter-Flotte gefangenen Flundernmengen. Beide Tabellen geben ein deutliches Bild von der gewaltigen Aufwärtsentwicklung, die die Flundernfischerei in den letzten Jahren genommen hat und von der grossen Bedeutung, die sie heute erlangt hat.

Das Laichgebiet des Flundernbestandes der südöstlichen Ostsee liegt in der Danziger Bucht. Schon im Herbst treten die Flundern die Wanderung von der Küste nach der Danziger Mulde an und laichen in der Zeit von Ende März bis Anfang Juni. Nach dem Ablaichen wandern die Flundern wieder auf ihre in Küstennähe gelegenen Weidegründe zurück.

Bereits Mitte Juni beobachtete ich im Jahre 1937 in losgerissenen Enteromorpha- und Cladophoramassen, unmittelbar am Ufer, die jüngsten Bodenstadien der Flunder. An den Küsten Gotlands und Fåröns stellte Hessle (1930) fest, dass selbst während der ersten Julihälfte (1929) die Flundernlarven noch nicht in grösserer Zahl zum Bodenleben übergegangen waren und erst am 21. und 22. August konnte dort eine geringe Anzahl der 0-Gruppe erbeutet werden. Wahrscheinlich ist der südbaltische Küstenstrom, der aus der Danziger Bucht kommt und in der Regel westöstlich gerichtet ist, die Ursache für das verhältnismässig frühe Auftreten der jungen Flundern an der Samlandküste. Die Eier und Larven werden offenbar von dem für die gesamten fischereilichen Verhältnisse der Samlandküste so wichtigen Strom erfasst und der Küste zugetrieben.

II.

Das gesamte Untersuchungsmaterial der Altersgruppe 0 wurde mit einem Schiebehamen in einer Wassertiefe bis zu 1 Meter im Hafen von Neukuhren gefangen. Die Fänge wurden bei günstiger Witterung an ein oder zwei Tagen eines jeden Monats ausgeführt und die jungen Flundern sogleich in 4 % Formol-Seewasser konserviert.

Altersgruppe I wurde im Mai ebenfalls mit einem Schiebehamen unmittelbar auf dem flachen Strande in der SW.-Ecke des Hafens von Neukuhren erbeutet. Die Juni-Probe wurde zum Teil gleichfalls mit einem Schiebehamen, zum Teil mit einer sogenannten Sutterwade, einem Zugnetz, das den Fischern zum Fang von Sandpierlingen dient, gefangen. Im Monat Juli konnte die Altersgruppe I nicht mehr auf den flachen Sandbänken beobachtet werden; mit dem Schiebehamen wurde nur noch Altersgruppe 0 gefangen.

Zum Vergleich steht eine Probe zur Verfügung, die am 20. September auf einer Poseidonfahrt mit einer Granatkurre in etwa 9 m. Wassertiefe vor der Kurischen Nehrung erbeutet wurde.

Die Längenmessungen, die Nahrungsuntersuchungen und die Wirbelzählungen wurden nach den üblichen Methoden ausgeführt. Das Durchschnittsgewicht jeder Probe wurde aus dem Gesamtgewicht der in Fliesspapier getrockneten Fische und der Individuenzahl berechnet.

III.

Die erste Probe der 0-Gruppe (1937) wurde am 23., 24. und 25. Juni 1937 im Hafen von Neukuhren, unmittelbar am Ufer, in 5—10 cm. Wassertiefe zwischen den mit Cladophora und Enteromorpha bewachsenen Steinen und zwischen den losgerissenen und vom Wellenschlag

hin und her bewegten Algenmassen gefunden. Auch im Juli halten sich die jungen Flundern noch in den Algenmassen auf; von August ab werden sie dann vorwiegend auf dem Sand, unmittelbar am Ufer, angetroffen.

In Tabelle 3 sind die Längen der jungen Flundern aller Proben, auf Intervalle von 5 mm. verteilt, angegeben.

Tabelle 3.

Das Wachstum der 0-Gruppe.

Fangzeit	Datum Monat	23.—25. Juni	10. Juli	5. August	13.—16. September	8. Oktober	11. November
Anzahl		105	690	518	410	235	119
Länge in mm.	10·0—15·5	75	46	2	—	—	—
	16·0—20·5	29	197	51	—	—	—
	21·0—25·5	1	275	138	8	8	—
	26·0—30·5	—	141	126	24	25	7
	31·0—35·5	—	29	97	68	41	13
	36·0—40·5	—	1	64	103	44	23
	41·0—45·5	—	1	30	85	58	31
	46·0—50·5	—	—	4	60	20	13
	51·0—55·5	—	—	2	36	17	11
	56·0—60·5	—	—	—	19	11	9
	61·0—65·5	—	—	—	8	7	5
	66·0—70·5	—	—	—	2	3	3
	71·0—75·5	—	—	—	1	—	2
	76·0—80·5	—	—	—	—	—	1
	81·0—85·5	—	—	—	—	1	1
	86·0—90·5	—	—	—	—	1	—
Durchschnittl. Länge in mm...		15·7	23·1	29·6	42·1	42·6	42·7
Durchschnittl. Gewicht in g...		0·05	0·17	0·37	0·95	0·99	1·01

Die Zusammenstellung zeigt deutlich, wie die einzelnen Fische des gleichen Jahrganges schon im Laufe der ersten Lebensmonate auseinanderwachsen. Im Juni sind nur Fische von drei Längenintervallen vorhanden, während sich die Längen im Oktober und November bereits über zwölf Intervalle ausdehnen. Die Verteilung der Individuen jeder monatlichen Probe auf die einzelnen Längenintervalle entspricht der Gauss'schen Fehlerkurve. Im Juni und Juli scheinen allerdings die kleinsten Individuen in den Proben zu fehlen.

Noch deutlicher zeigt die graphische Darstellung der Durchschnittswerte für Längen und Gewicht in den einzelnen Monaten den Verlauf des Wachstums (Abb. 1).

Von Mitte Juni, nachdem die jungen Flundern zum Bodenleben übergegangen sind und in grosser Zahl am Strande beobachtet werden können, bis zum Monat September steigen die Längenwachstums- und Gewichtskurve etwa im gleichen Masse steil an. Im September hört dann das Wachstum und die Gewichtszunahme praktisch ganz auf.

Auf diese Erscheinung wird später, bei der Betrachtung der Ernährung der jungen Flundern, noch wieder zurückzukommen sein.

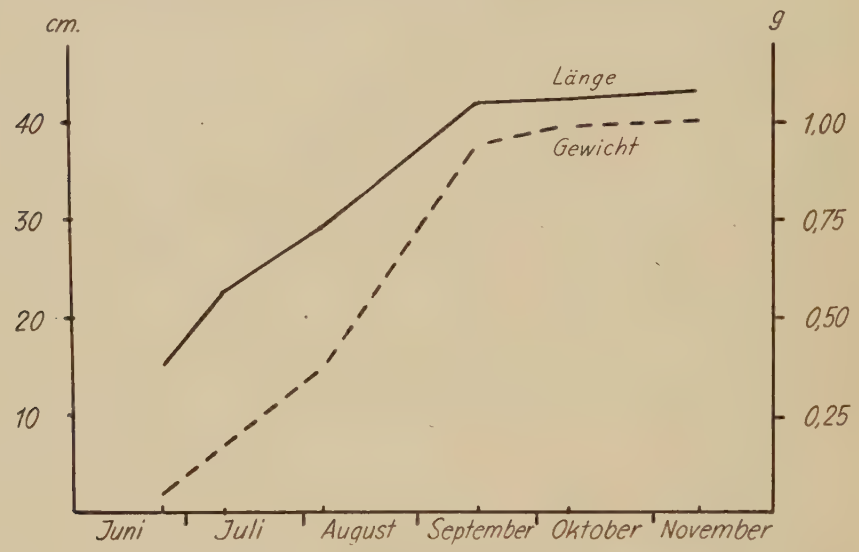

Abb. 1. Die Längen- und Gewichtszunahme der Altersgruppe 0 in den Monaten Juni bis November.

Drei Proben der Altersgruppe I, die in den Monaten Mai, Juni und September gefangen wurden, geben einen Einblick in das Wachstum der jungen Flundern in ihrem zweiten Lebensjahre.

Tabelle 4.

Das Wachstum der I-Gruppe.

Fangzeit Datum Monat		7.—9. Mai	24.—26. Juni	20. September
Fangort Gerät		Neukuhren—Hafen Schiebehamen,	Sutterwade	Kurische Nehrung Garnelen Kurre
Anzahl		33	80	162
Länge in mm.	31·5— 40·5	13	—	—
	41·0— 50·5	12	1	—
	51·0— 60·5	6	10	1
	61·0— 70·5	2	23	3
	71·0— 80·5	—	29	33
	81·0— 90·5	—	13	57
	91·0—100·5	—	2	40
	101·0—110·5	—	—	21
	111·0—120·5	—	2	5
	121·0—130·5	—	—	2
Durchschnittl. Länge in mm.		45·4	73·1	90·3
Durchschnittl. Gewicht in g.		—	4·5	7·5

In vorstehender Tabelle sind die Individuen der einzelnen Proben auf Längenintervalle von 10 mm. verteilt, so dass die Längenzunahme von Monat zu Monat wieder sehr deutlich hervortritt. Ein Vergleich der Durchschnittswerte für die drei Monate zeigt weiterhin, dass das Längenwachstum ausserordentlich rasch ist und das durchschnittliche Gewicht in drei Monaten um etwa drei Gramm gestiegen ist.

Um das Wachstum der Flunder weiterhin verfolgen zu können, sind die untermassigen Jungfische, die mit den Marktflundern im Grundschleppnetz gefangen wurden, untersucht worden. Da, wie die folgende Tabelle zeigt, das Wachstum im vierten Lebensjahre verhältnismässig gering ist, verwischen sich die Grössenunterschiede der einzelnen Altersgruppen und machen eine Bestimmung des Alters erforderlich. Es zeigte sich ferner, dass für das durchschnittliche Gewicht und die durchschnittliche Länge der Altersgruppen II und III sehr verschiedene Werte herauskamen, je nachdem, ob die Durchschnittswerte aus den untersuchten untermassigen Fischen oder den Marktflundern errechnet wurden.

Neben den Unterschieden im Wachstum von Fangplatz zu Fangplatz beginnen sich auch bereits bei der Altersgruppe II die Wachstumsunterschiede von Männchen und Weibchen herauszubilden.

Tabelle 5.

Fangplatz			Vor der Kur. Nehrg.	Vor der Kur. Nehrg.	Vor Neukuhren	Cranzer Loch	Vor Memel
Tag			18.6.37.	22.7.37.	16.8.37.	13.9.37.	14.10.37.
Anzahl			798	410	173	382	343
Altersgruppe II	Länge in cm.	♂♂	16·2	16·2	17·2	20·6	21·3
		♀♀		16·5	17·0	20·8	21·3
	Gewicht in g.	♂♂	49·0	49·0	57·0	110·5	112·6
		♀♀		50·0	56·0	116·7	138·2
Altersgruppe III	Länge in cm.	♂♂	17·3	17·4	18·4	23·2	24·2
		♀♀		17·7	17·3	25·3	25·7
	Gewicht in g.	♂♂	50·5	51·0	56·0	140·4	149·7
		♀♀		52·0	57·0	201·4	224·4

Während die drei Proben von 18. 6., 22. 7. und 16. 8. vorwiegend aus untermassigen Flundern bestanden, wurden am 13. 9. und 14. 10. nur Marktflundern untersucht, so dass die in der Tabelle 5 angegebenen Zahlen nur Annäherungswerte für das Längenwachstum und die Gewichtszunahme der Flundern im zweiten und dritten Lebensjahre zu geben vermögen.

IV.

Von jedem monatlichen Fang wurden an 20—60 Fischen aller Grössen Nahrungsuntersuchungen durchgeführt. In der folgenden Tabelle ist die Anzahl der Flundern (in %) angegeben, in denen die einzelnen Nährtiere gefunden wurden.

Tabelle 6.

Die Nahrung der Altersgruppe 0 zusammengestellt nach der Anzahl der Flundern (in %), in denen die einzelnen Nährtiere gefunden wurden.

Monat	Juni	Juli	August	September	Oktober	Nóvember
Anzahl der unters. Fische	21	42	44	51	49	62
Anzahl der Flundern mit bestimmb. Nahrg.	20	40	40	40	37	30
Nereis diversicolor ...	—	—	2·5	5·0	10·8	3·3
Oligochaeten	16·8	95·0	37·5	7·5	—	16·6
Mysis mixta	—	—	15·0	20·0	8·1	10·0
Gammarus locusta	—	—	5·0	10·0	32·4	10·0
Chironomiden Larven u. Puppen ..	5·0	35·0	80·0	25·0	32·4	23·3
Idothea viridis	—	—	—	5·0	51·4	—
Harpacticidae	100·0	62·5	45·0	72·5	78·4	73·3
Neritina fluviatilis ...	—	—	—	—	5·4	—
Hydrobia baltica	—	—	—	—	18·9	10·0
Mytilus edulis	—	—	—	—	5·4	—
Cladocera	—	7·5	—	—	—	—
Rotatoria	10·0	—	—	—	—	—
Bodendiatomeen	25·0	40·0	32·5	47·5	37·8	3·3
Enteromorpha Cladophora	20·0	10·0	10·0	12·5	35·1	—

Tabelle 7.

Prozentuale Zusammensetzung der Nahrung (nach Anzahl der Nährtiere) von Flundern des ersten Jahrganges.[1])

Monat	Juni	Juli	August	September	Oktober	November
Anzahl der unters. Fische	21	42	44	51	49	62
Anzahl der Fische mit bestimmb. Nahrg.	20	40	40	40	37	30
Durchschnittl. Anzahl d. Nährtiere i. Fisch	5	9	17	15	11	9
Nereis diversicolor ...	—	—	0·1	0·4	1·0	0·3
Oligochaeten[1])	17	64	18	8	—	18
Mysis mixta	—	—	2·6	11·3	4·9	1·0
Gammarus locusta	—	—	0·3	1·0	12·3	1·4
Chironomiden Larven u. Puppen ..	0·9	10·3	72·2	8·4	10·1	4·8
Idothea viridis	—	—	—	0·4	25·3	—
Harpacticidae	78·5	24·3	7·2	70·8	40·5	68·2
Neritina fluviatilis ...	—	—	—	—	0·7	—
Hydrobia baltica	—	—	—	—	2·9	5·5
Mytilus edulis	—	—	—	—	2·2	—
Cladocera	—	1·1	—	—	—	—
Rotatoria	3·7	—	—	—	—	—

[1]) Da die Zahl der Oligochaeten sich nicht immer mit der erforderlichen Genauigkeit feststellen liess, sind die angegebenen Prozentsätze nur Annäherungswerte.

Beide Tabellen zeigen die überragende Bedeutung der Harpacticiden für die Ernährung der Flunder des ersten Jahrganges. Im Juni wurden daneben hauptsächlich Grünalgen und Bodendiatomeen gefunden. Im Juli treten die Oligochaeten an die erste Stelle; 95 % der Flundern hatten Oligochaeten gefressen und 63 % Harpacticiden. Chiromidenlarven und Puppen machen im August 72 % der gefundenen Nährtiere aus. Im September sind es wieder die Harpacticiden, die an die erste Stelle rücken, während die Oligochaeten und die Chiromidenlarven und Puppen nur in geringen Mengen gefunden wurden. Auch in den Monaten Oktober und November überwiegen die Harpacticiden.

Im allgemeinen besteht die Gesetzmässigkeit, dass kleinere Nährtierarten von kleineren und jüngeren Flundern gefressen werden, während grössere und ältere Individuen auch die grösseren Nährtierarten bevorzugen. Rotatorien und Cladoceren wurden nur im Juni bezw. Juli beobachtet; *Nereis, Mysis, Neritina* und *Gammarus* hingegen erst von August ab, nachdem die Flundern bereits eine bestimmte Grösse erreicht haben, um so grosse Tiere zu bewältigen.

Das Verhältnis der Anzahl der untersuchten Fische zur Anzahl derjenigen Fische, in denen bestimmbare Nahrungsreste gefunden wurden, ist während des ersten Sommers nicht konstant. Die Tabelle 6 zeigt, dass die Anzahl der Fische, die "leer" oder mit unbestimmbaren Nahrungsresten im Magen und Darm gefunden wurden, von September

Tabelle 8.

Die Nahrung der Altersgruppe I zusammengestellt nach der Anzahl der Flundern (in %), in denen die einzelnen Nährtiere gefunden wurden.

Monat	Mai	Juni	September
Anzahl der unters. Fische	33	40	49
Anzahl der Fische mit bestimmb. Nahrg.	31	40	40
Durchschnittl. Anzahl d. Nährtiere i. Fisch	9·9	17·0	17·0
Nereis diversicolor	22·6	20·0	70·0
Mysis mixta	80·6	45·0	5·0
Corophium volutator	22·6	7·5	—
Chironomiden Larven u. Puppen	6·5	55·0	—
Gammarus locusta	—	40·0	22·5
Neritina fluviatilis	—	32·5	—
Hydrobia baltica	—	—	10·0
Mytilus edulis	—	—	7·5
Cardium edule	—	—	22·5
Idothea viridis	—	7·5	—
Oligochaeten	9·7	37·5	—
Crangon vulgaris	—	—	25·0
Sphaeroma rugicaudum	—	2·5	—
Harpacticidae	29·0	15·0	—
Cladophora, Enteromorpha ...	3·2	5·0	—

an stark ansteigt und dass im November kaum 50 % der untersuchten Fische Nahrung zu sich genommen hatten.

Auch die durchschnittliche Anzahl der Nährtiere in einem Fisch ändert sich, und zwar etwa im gleichen Sinne wie der Prozentsatz der Fische ohne Nahrung. Das Maximum mit 17·4 Nährtieren in einem Fisch wird im August erreicht; im September sind es noch 15 und im November nur noch 9 Nährtiere, die durchschnittlich in einer Flunder gefunden wurden.

Die Betrachtung der Längen- und Gewichtskurven hatte gelehrt, dass ab September weder eine Längen- noch eine Gewichtszunahme stattfindet; hier erkennen wir nun die Ursache dieser Erscheinung: eine Einschränkung der Nahrungsaufnahme.

Betrachten wir nun die Ergebnisse der Nahrungsuntersuchungen an den Flundern der Altersgruppe I (Tabelle 8), so ist zunächst einmal hervorzuheben, dass während der Monate Mai und Juni, solange die Flundern also noch unmittelbar in der Nähe des Ufers auf den flachen Sandbänken leben, kein grosser Unterschied bei einem Vergleich mit der Ernährung der Altersgruppe 0 während der Herbstmonate in Erscheinung tritt.

Es sind eine Reihe von Nährtieren hinzugekommen, die bei der Altersgruppe 0 noch nicht beobachtet wurden (*Corophium, Spaeroma*) und insbesondere die grösseren Nährtiere (*Nereis, Mysis, Corophium, Gammarus*) treten in höheren Prozentsätzen auf, während die Harpacticiden, die im ersten Sommer mit die Hauptnahrung der jungen Flundern bilden, nicht in so grosser Zahl mehr beobachtet wurden.

Mit dem Abwandern der Flunder in grössere Tiefen (4 bis 10 m.) tritt auch eine Änderung in der Ernährung ein; *Nereis, Crangon, Cardium* und *Gammarus* sind nun die wichtigsten Nährtiere. Mit der Änderung des Nahrungsangebotes läuft die Umstellung der Flunder auf die neuen Ernährungsbedingungen parallel.

Zum Vergleich seien abschliessend noch die Ergebnisse der Untersuchung einer Probe von Marktflundern wiedergegeben, die am 1. Juli 1937 auf dem Flundernfangplatz "Cranzer Loch" gefangen wurden:

Tabelle 9.

Anzahl der untersuchten Fische	davon mit bestimmbarer Nahrung	Anzahl Nährtiere je Flunder
46	37	38·2
Nährtiere	Anzahl der Flundern (in %) in denen die einzelnen Nährtiere gefunden wurden	Anzahl der gefundenen Nährtiere in %
Tellina	100·0	60·0
Polychaeten	51·3	5·3
Mysis	27·0	7·9
Mesidothea	45·9	3·9
Corophium	64·8	12·6
Mytilus	5·4	5·6
Cardium	45·9	4·0
Hydrobia	13·5	0·5
Crangon	5·4	0·1

V.

Die Untersuchungen über die Variabilität der Wirbel- und Flossenstrahlen der Jungflundern von der Samlandküste sind gleichfalls nach Jahrgängen getrennt vorgenommen worden.

Es handelt sich wieder um den Jahrgang 1936, der als Altersgruppe I in den Monaten Mai und Juni 1937 und um den Jahrgang 1937, von dem eine Probe (Altersgruppe 0) am 5. August 1937 im Hafen von Neukuhren gefangen wurde.

Das Ergebnis der Wirbelzählungen geht aus der folgenden Tabelle hervor:

Anzahl der Wirbel (Vert. S.)

	n	34	35	36	37
Altersgr. I	112	2 (1·8%)	16 (14·3%)	57 (50·9%)	37 (33·0%)
Altersgr. 0	500	4 (0·8%)	76 (15·2%)	290 (58·0%)	127 (25·4%)

	38	M ± m
Altersgr. I	—	36·152 ± 0·068
Altersgr. 0	3 (0·6%)	36·098 ± 0·003

Die auftretenden Differenzen sind zufällig und wohl auf die verhältnismässig geringe Individuenzahl der untersuchten Altersgruppe I zurückzuführen.

Bekanntlich nimmt die durchschnittliche Wirbelzahl, von lokalen Abweichungen abgesehen, in der Ostsee von Westen nach Osten zu. In der westlichen Ostsee beträgt die Wirbelzahl 35·28, auf der Oderbank 35·63 und nach den Untersuchungen von Mannsfeld (1934) bei Libau 36·22 und bei Windau 36·23. Die durchschnittliche Wirbelzahl der an der Samlandküste gefangenen Flundern liegt mit 36·10 Wirbeln zwischen der pommerschen und lettländischen Küste und reiht sich damit ohne Abweichung in die erwähnte Gesetzmässigkeit ein.

Grösser sind die Unterschiede, die zwischen den Flossenstrahlenzahlen der beiden Jahrgänge bestehen: —

Analflossenstrahlenzahlen.

	n	35	36	37	38	39	40	41
Altersgr. I	112	—	3	3	26	27	18	18
%		—	2·7	2·7	23·2	24·1	16·1	16·1
Altersgr. 0	500	4	5	14	44	100	105	130
%		0·8	1·0	2·8	8·8	20·0	21·0	26·0

	42	43	44	45	46	M ± m
Altersgr. I	10	3	3	—	1	39·687 ± 0·170
%	8·9	2·7	2·7	—	0·9	
Altersgr. 0	66	21	8	2	1	40·206 ± 0·073
%	13·2	4·2	1·6	0·2	0·2	

Die Unterschiede in der prozentualen Verteilung der Individuen auf die einzelnen Merkmalwerte sind ganz beträchtlich; jedoch ist die Differenz zwischen beiden Mittelwerten kleiner als der dreifache mittlere Fehler der Differenz (0·519 ± 0·185). Ein wirklicher, mathematisch nachweisbarer Unterschied ist in der Analflossenstrahlenzahl zwischen beiden Jahrgängen also nicht vorhanden. Die Differenzen werden auch in diesem Falle wohl dadurch bedingt sein, dass die Probe der Altersgruppe I nur aus 112 Individuen bestand.

VI.

Eine besondere Aufmerksamkeit wurde den Wirbelverwachsungen gewidmet. Bei den Flundern der Altersgruppe I wurden bei 24 % und bei denen der Altersgruppe 0 bei 29 % aller untersuchten Fische Verwachsungserscheinungen am Achsenskelett beobachtet.

Über die Häufigkeit der komplexen Verwachsungen gibt die folgende Tabelle Auskunft:

Komplexe Verwachsungen.

Vert. S.	Altersgr. I		Altersgr. 0	
34	2	100 %	4	100 %
35	8	50 %	42	55 %
36	8	14 %	75	26 %
37	—	—	9	7 %
38	—	—	—	—
	18	16 %	130	26 %

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Laboratory Apparatus for the Rearing of Young Salmon from Freshly Fertilized Eggs.

By

Frank H. Moult,

Department of Zoology, University of Liverpool.

THE simple apparatus described below has been successfully used in this Department for the rearing of salmon from freshly spawned eggs. The technique employed in large-scale fish hatcheries has been modified to conform with laboratory conditions and the mortality rate, whilst in the apparatus, has been so exceptionally low (less than 0·5 %) that the method seems worth recording.

The apparatus consisted essentially of a deep perforated zinc tray supported inside a glass tank. The eggs were freely spaced in a single layer on the base of this tray, and a continuous stream of aerated water was directed over them.

Figure 1 shows a section and a plan of the apparatus to be described, the size shown being suitable for up to two thousand salmon eggs.

The outer sides of the glass tank A were covered with black paper to prevent lateral lighting. A detachable lid, made of "Windolite" screwed to a wooden frame, was fitted to the top of the tank above the tray. This admitted light from above while excluding dust.

The tray B was constructed from perforated zinc (perforations $^1/_{16}$" diam.). Since it was considered desirable to exclude all metals except zinc, the seams at the corners of the tray were not soldered but were stitched together with zinc wire. The tray was elevated by stitching to its base two strips, C, of perforated zinc, folded to be ⊓ in section. By prolonging these supports to the ends of the tank the tray was also fixed in position. All zinc surfaces were finally covered with several coats of a black bituminous varnish, which was then allowed to harden for four or five days.

A glass plate K was placed at one end of the tank, resting on the supports of the tray and leaning at an angle against the end of the tank.

Ordinary tap water, at a temperature varying between 5° C. and 9·25° C. (mean approx. 6·64° C.) was supplied at a rate of

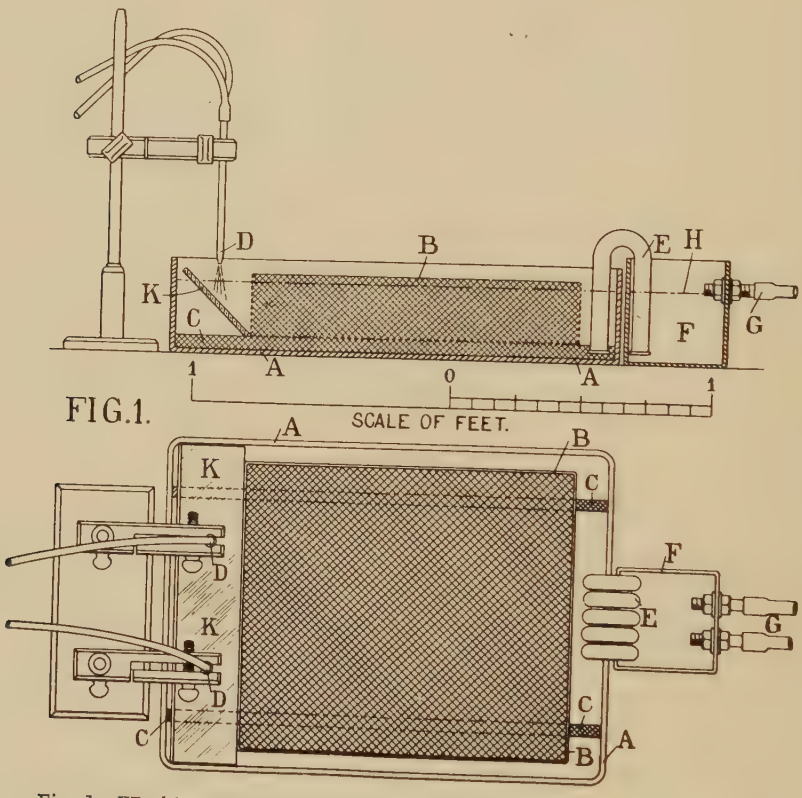

FIG.1.

Fig. 1. Working drawings of apparatus: above, section; below, plan.

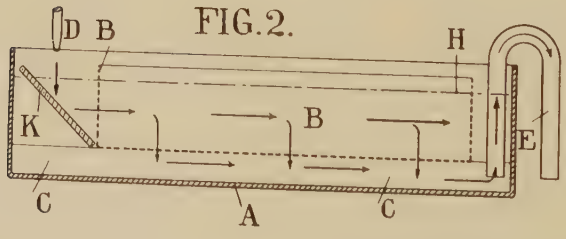

FIG.2.

Fig. 2. Diagram to show the main circulation.

approximately one gallon per minute through two fish-tail jets D. These jets were fixed above the glass plate K, which served to deflect the incoming current through the end of the tray and over the eggs. Sufficient aeration was effected by the two sprays striking the surface of the water and carrying down a large number of small air bubbles.

Water was drained from beneath the tray through the five siphons E, of ½″ bore, into the auxiliary tank F, from which it escaped via two rubber pipes G of ¾″ bore. This auxiliary tank was constructed from a tin box liberally coated with bituminous varnish to prevent rusting. By raising or lowering this box the water level H in the main tank could be correspondingly adjusted, the most suitable level being about half an inch below the upper edge of the tray.

It will be seen from Figure 2 that, on entry, the current of water strikes the deflector plate K, passes *over* the eggs and is drawn *down* through the *base* of the tray B by the siphons E. In this way each egg is bathed in a constant stream of oxygenated water. The siphons should *not* draw water through the *end* of the tray, but should collect the lower layer from beneath it. This latter condition may be verified before use by means of a suspension of finely powdered chalk.

As a precaution against the effect of any toxic substances dissolved from the bitumen, the apparatus was in operation for several days before being used.

The eggs were installed a few hours after being spawned and were then not disturbed in any way until they hatched, when the empty egg capsules were removed.

The young fish were reared in the apparatus here described up to the age of four months. They were then transferred to a large tank and feeding was commenced.

From the age of 17 weeks to 53 weeks they were given finely minced raw liver. The mincer used had a cutting disk with holes of 2 mm. diameter. After 53 weeks similarly minced beef was substituted on alternate days, and minced earthworm was also added very occasionally.

The original stock, spawned in November 1937, has been maintained in this Department to the present time. A second stock, spawned the following year, has also been hatched in the same apparatus with equal success.

I wish to express my thanks to Mr. G. M. K i n g, Superintendent and Manager for the Dee Fisheries Board, for allowing me to see the methods used in the Board's hatchery at Llandrillo and for providing the eggs used in the experiments.

Reviews.

Ed. Le Danois. "L'Atlantique, Histoire et Vie d'un Océan. Sciences d'Aujourd'hui." 290 pp., 16 pl., 54 figs. Alb. Michel, Paris, 1938.

More than a quarter of a century has elapsed since Gerhardt Schott published his celebrated monograph, "Geographie des Atlantischen Ozeans". The present volume on the Atlantic often reminds the reader of its predecessor, especially in the description of the various geographical subdivisions of this ocean, though much has been added, thanks to the enormous development of new scientific methods.

Gradually, out of the subconscious feeling of isolation and horror with which primitive man first faced the dreary, endless waste of waters around the habitable world, there rose the invincible inquisitiveness, the mother of all science, that enticed men to venture out to the ever receding horizon and to geographical discoveries which, beginning with tentative efforts in the nursery school of the Mediterranean, finally led our race to the shores of West Africa and America. These endeavours, and the dawn of oceanographical science, its phenomenal growth, urged on by the technical achievements of the modern age, are described in the introduction of the volume under review.

We next proceed to the description of the Atlantic proper, and, thanks to the efforts of generations with sounding machines of the Leblanc, Kelvin and Lucas type, greatly improved upon by the ultrasonorous and sonorous echo-sounding, we get an imposing geographical review of the ocean floor, the backbone of which is the famous Atlantic ridge, flanked on both sides by the deep basins (John Murray's "deeps"), separated by more or less developed ridges. This general survey of the configuration of the ocean floor as we view it with the mental eye is itself an introduction to a fascinating chapter on the genesis of the Atlantic throughout the geological ages. We are introduced to the old problem, whether the deep ocean basins are permanent, or not. The latter theory was hold by those scientists who could not explain the present distribution of living beings and of analogous geological formations in widely separated tracts of land otherwise than by postulating land bridges that rose out of the waves and foundered again in the course of time. Attractive as this hypothesis is, it contains so many elements of uncertainty that the present general attitude of science has welcomed the ingenious theory of Wegener, according to which in the Carboniferous age all the present

continental land masses were packed together into a continuous continent, welded around a South Pole somewhere south of Madagascar, and gradually becoming separated. We visualize the sial floes, floating like enormous icebergs upon the specifically heavier sima magma, and, forced asunder, by their very drift creating oceans out of which long drawn-out trails of land emerge and submerge again, till at last the picture of our world is reached with which we are all familiar. The French author, though by no means denying the merits of Wegener's hypothesis, prefers another explanation, based on Suess's assumption of an Arctic and an Antarctic continent of Primary age, separated by a world-encircling ocean, the Tethys, which by the raising of mountain chains in the geosynclinals was gradually broken in its continuity, until the final geographical arrangement arose. The history of the transverse land connexions across the Atlantic (boreal, North Atlantidean, equatorial and Archhelenis bridge), the subsidence of which still leaves traces of their former existence in the form of submarine ridges and volcanic islands, is briefly but clearly treated.

We are likewise given an excellent account of the renowned Platonic Atlantis, which in Cretaceous or perhaps Eocenen times should have existed somewhere between the Antilles and Morocco and disappeared towards the Miocene, leaving such shelves as those of Madeira and the Canaries, on which various submarine banks rise more or less steeply out of oceanic depths.

There are also many interesting details, illustrating the increase of our knowledge since the publication of Schott's memorable treatise on the Atlantic. We can only refer briefly to the genetic history and the present structure of various Atlantic areas; the seas around the primeval Scandinavian nucleus, in which, of course, the pleistocene glaciations figure largely; the Franco-British shelf, in which account the North Sea is included. Numerous traces of submarine river valleys ("thalwegs") are recorded here as continuations of present-day rivers.

Tectonic ruptures brought about the flooding of great areas, some of which have been recorded even in historical times. Further south, in the Bay of Biscay, and, of course, still more pronounced in the Mediterranean basin, alpine folds since the Eocene caused considerable geographical changes. After describing the region around the Canadian Shield (Banks of Newfoundland and Nova Scotia, and Maine), one of the most stable portions of the earth's crust and connected with the Huronian folding and the Antillean Sea, that highly vulcanic western "Mediterranean", incorporated in the Atlantic only by the closing of the passage between Yucatan and Panama, the author closes his review of Atlantic regions with the Antarctic Antilles, a chain of archipelagoes stretching from the Falklands along South Georgia, South Sandwich, etc. to the Graham peninsula, and with a final account of the genesis of these equatorial and Antarctic sweeping curves of volcanic chains of islands. Their history, with those of similar formations in the Pacific, is based on the rising of a continental barrier in the west, a subsidence of the basin to the east, and the creation of an insular chain along the eastern border. In this way the ancient Tethys was broken up by various basins of volcanic origin, the shallower parts of which tend to become filled with sediments in the course of aeons.

The second part of the book deals, first, with the chemical composition of sea water, the temperature, salinity and oxygen content; with the principle of practical incapability of waters of different character becoming mixed, with the troposphere and stratosphere of Defant and Wüst, and with the classification of Atlantic waters. For simplicity, a division between

tropical and polar (or boreal) waters, characterized by their salinity, and each of them (the latter especially) subdivided, was adopted. The next chapter deals with oceanic circulation: expansions of the more mobile tropical waters over and between layers of the more passive polar front. Here we encounter the personal and original views of the author. He tells of his first conceiving the idea of periodical expansions of Atlantic water in 1921 in the inner parts of the Bay of Biscay, demonstration of a phenomenon that had been compared by Pettersson in former years to pulsations of the ocean, and afterwards to internal tidal waves. The French author styled them "transgressions". We, of the eastern Atlantic, are now familiar with the periodic retreat of tropical waters in winter and their gradual expansion towards the north in summer, reaching generally beyond Bear Island. In the southern hemisphere there is a similar, though much more regular, line of minimum and maximum expansion. The point of departure of these movements lies apparently in the equatorial belt, at a depth of about 300 m., very poorly oxygenated, from which at times thick layers of high salinity (more than 35 $^0/_0$) expand towards higher latitudes, and on the continental shelf surface layers of high temperature follow in their wake. It is most interesting to watch the course of these expansions, which follow the deeper valleys of the ocean floor.

But the real activating factor is cosmic, as has been explained by Pettersson and others: this cause is a complicated combination of lunar and terrestrial periods, variations in terrestrial magnetism and latitudinal displacements of solar spots. The maximum in the periodicity of all these factors is defined by the coincidence of synodic and anomalistic periods of the perihelium phase of the earth with a maximum declination of the moon. Maxima occur at an interval of 111 years, smaller ones at a fraction of this number. So we get intervals of 18·6, 9·3 and 4·6 years, each of these decreasing in amplitude. The last biggest maximum occurred in 1885, and it may be calculated that the next octo-decimal maximum, according to previous experience, will be due in February 1940. Indeed, this whole theory fits well with observations of large-period fluctuations of herring fisheries in the Skagerak over many centuries, and with investigations of the oceanic expansions themselves over the last fifty years or so.

Before proceeding to the discussion of the mechanism of these oceanic expansions the author surveys the great Atlantic currents and here the general prevailing opinion about the thrust of the Gulf Stream is modified to bring it into line with modern conceptions of the Atlantic drift. In a subsequent chapter the expansions in certain parts of the North Atlantic are studied. There is, of course, a periodically acting driving force, of more equatorial character and, before it, another one of Atlantic water (different in salinity and temperature) and, as a counterpart, a polar (boreal) front, on either the American or the European side.

One would like to deal at greater length with the local behaviour of these expansions: with the interplay of the polar front and the equatorial waters near the Newfoundland Bank, the expansion of the latter waters off the Moroccan coast, the invasion by Atlantic waters of the Bay of Biscay and the Franco-British shelf, their struggle with polar waters in the Norwegian Sea and off the American coast—but space forbids.

The first chapter of the next section contains rapid sketches of bionomic classification of marine animals, their ecological reaction to hydrological factors, migration and marking of fish, ichthyometry, and biological equipment for investigation. The next chapter describes the importance of oceanic

expansions to seasonal fisheries. Obviously these periodic invasions of Atlantic water must call forth specific reactions in certain fishes and other marine animals, for one group may inhabit the warmer waters of higher salinity, while other beings eschew them and prefer a boreal environment. One could also say in a general way that there are oceanic and continental species, and we find the best instances among migratory fishes.

Of these the pelagic fishes are considered first. The best examples of positive Atlantic character are perhaps tunny, mackerel and pilchard. The herring, on the contrary, is a fish of the continental shelf. Whether a species is essentially oceanic or continental—to use these expressions—is decided to a certain degree at its time of ripening or spawning, and depends also on the age of the fish.

Two species of demersal fish are discussed: cod and hake. The first-named is an inhabitant of boreal waters and prefers low temperatures, according to the habitat of the various races. Its responses to temperature before and during spawning time and during the period of dispersion are best studied in the region of the Newfoundland Bank, where temperatures of 4° are preferred by the cod. In seasons that show a departure from the ordinary temperature at a depth of 35 m. and when the cod fishery fails locally, there is a chance of remunerative fishery in Davis Strait. In contrast to the cod, and to most of the other commercial Gadoids, the hake inhabits the continental slope at a certain depth and is guided in its movements by a required high salinity, defined by the expansion of oceanic waters.

The case of anadromous and catadromous fishes is exemplified by the behaviour of salmon and eel, in which the negative or positive influence of the advance or retreat of oceanic waters, and the reaction thereon of the boreal front, is again demonstrated. It is worth noticing that the long voyage of eel larvae across the Atlantic (4·5 years) agrees in duration with periodical excesses of amplitude in the oceanic expansions which are mentioned before in the discussion of their cause.

In a review like this, it is impossible to render adequate justice to the treasure of information offered by this handbook. Written in an admirable style, sometimes striking a humorous or mildly ironic note, sometimes even poetical, it bears witness to the author's versatility and width of interests. In view of this, an occasional lapse (as the bottom of p. 261, in which it is said that a green colour on the disk of the plankton indicator is *favourable* to the herring etc. ....) is readily forgiven.

J. J. T.

A. Defant. "Aufbau und Zirkulation des Atlantischen Oceans". Sitzungsber. Preussischen Akad. Wiss., Phys.-math. Kl. 1938, XIV, S. 1—29, Abb. 7, Taf. 7. Berlin, 1938.

This most useful paper consists of a complete summary of the results published in Volume VI of the "Meteor" reports. It will be welcomed by all oceanographers. Those whose interests are primarily biological or chemical will find a concise account of the circulation of the Atlantic Ocean as developed during recent years by investigators at the Institut für Meereskunde. Specialists in the problem of ocean circulation will profit by this opportunity to consider carefully the essential principals on which the analysis of the "Meteor" observations depends.

If there has been any weakness in the "Meteor" reports, it has been caused by the very large number of observations that had to be studied. Thus it was necessary to subdivide the material and to publish the results over a considerable period of years. In reporting on the circulation of the troposphere layer separately from that of the stratosphere, it may have seemed to some oceanographers that the German investigators were too confident of their basic assumption that the circulation in these two layers is to some extent independent. However, D e f a n t in this new paper presents a very strong case for the plan within which he and his collaborators have worked up their data. In short, this general account of the structure and circulation of the Atlantic Ocean is perhaps almost more convincing than are the several detailed papers on which it is based.

C. O'D. I.

H. Thomsen. "Hydrography of Iceland Waters." Zoology of Iceland, Vol. I, Pt. 4, pp. 36, 22 figs., 1 Plate. Copenhagen and Reykjavík, 1938.

This paper is a brief and clear account of the hydrographical conditions of the waters surrounding Iceland. For more detailed information on some of the questions the reader is referred to former results, cited in the list of literature. Other questions are studied on the basis of numerous observations, collected from different vessels since 1903, primarily from the Danish research vessels "Thor" and "Dana"; most of these observations are to be found in the "Bulletin Hydrographique". The author of the paper has taken part in the research cruises in 6 different seasons since 1926.

After a short review of the bottom configuration, the currents and the tides, the surface water is studied partly by means of R y d e r's charts of surface temperature, based on observations from the years 1875—1915, and partly by means of surface observations from a number of coastal stations during the years 1924—1933. Then the characteristics of the deep water to the east, south, and west of Iceland are illustrated by means of three „Dana" stations.

The coastal water is studied first by means of observations throughout the year from the two stations "Akranes" and "Skagi" in Faxaflói outside Reykjavík, and then by sections seawards from Langanes, Vestrahorn, Selvogsbanki, Kögur and Siglufjödur, which are situated on the north-eastern, south-eastern, south-western, north-western, and northern parts of the coast. Four of these sections have been repeated in the different seasons of the year.

Finally the hydrographical conditions in three Icelandic fjords are studied (Isafjardardjup, Eyafjördur and Seydisfjördur), and lastly the conditions regarding oxygen and nutrient salts are shortly mentioned.

The study of the seasonal variations of the coastal water, at the stations outside Reykjavik and in the above-mentioned sections, exhibit features of considerable interest. The change from winter conditions with poor stability (more or less vertical isolines) to summer conditions with great stability (horizontal stratification) is clearly demonstrated. It seems that more investigations north of Iceland, for instance, along the section from Siglufjördur, would now be of special interest, because of the considerable changes appear-

ing here even in summer. A better knowledge of these changes may prove of great importance also to the fisheries.

On the whole this paper shows that the knowledge of the general features of the hydrographical conditions, including seasonal variations, in the waters around Iceland is now becoming fairly clear, a knowledge certainly of great importance to the fisheries and for the planning of further hydrographical investigations along the same line of research. If a more detailed picture of the conditions were required, involving as they do a complexity of different phenomena, many more investigations would certainly be needed.

Håkon Mosby.

H. U. Sverdrup. "On the Process of Upwelling." Journ. Mar. Research, Vol. I, No. 2, pp. 155—164, 7 figs. New Haven, Conn., 1938.

The oceanographic cruises of the vessel "Blue-fin" of the California State Fish and Game Commission, which form the subject of this paper, were run off Port San Luis on the Californian coast. They consisted of a single line of stations repeated three times within three months, but the observations made are not described. The cruises were happily situated with regard to meteorological conditions, the first on 25—27. March, 1937 occurred after a bout of heavy weather when the wind lay towards the coast. The second was made on 5—6. May after the wind had changed; it then blew from the N.N.W., a direction more or less parallel to the coast. The interesting consequences of these winds on the hydrology of the surface layers are examined.

The first was the onset of marked upwelling. It is shown on the second cruise by a marked contrast in the position of isopycnals and it is used as evidence that the surface current deviated from the coast in a manner to be expected from such wind. From the vertical displacement of temperature, salinity and oxygen Prof. Sverdrup deduces the vertical velocity and horizontal off-shore velocity of the current; and a maximum value of 11 cm./sec. (6 miles a day) for the latter is computed. The calculations which are promised in a future report are based on the assumption of uniform velocities parallel to the coast; but the actual conditions of wind and current as they were experienced on board ship are not given, and the relevant sections of temperature and salinity are not illustrated. The wind data were taken from the land station at San Diego some 250 miles distant and their correspondence with the actual conditions met with is taken for granted. The paper is thus one in which theory and argumentation take a prominent part.

Accessory water movements are described and are supported by isobaric considerations. In particular Prof. Sverdrup draws attention to "a transport away from the coast and a banking up off-shore of the light surface water"; he suggests that "it is probable that the transport is caused by wind", but he does not explain the mechanism of the banking up. The lines of stations were limited to 250 km. and shed no light on conditions in the open ocean. A banking up of the surface water seems to argue the existence of a convergence and possibly of less strong or even adverse winds over the ocean at large. The reader may see that the isopycnals at the outset of the investigation on 25—27. March betray the presence of slight upwelling in spite of the on-shore wind; but he is given no clue to decide whether it indicates a widespread southerly wind over the ocean at large and outside the locality under consideration. According to the Washington Pilot Charts,

this area lies slightly to the northward of the trade winds; in it the wind is prevalently N.W., N. and N.E., and would not therefore appear to be conducive to such banking up.

The circulation within the zone of upwelling is of the type that has often been found in such areas. A surface transport away from the coast is fed by vertical movement close inshore and by an undercurrent of compensation flowing towards the land. As in other areas, so here, mixing is intensive close to the coast whereas off-shore the water is layered. Prof. Sverdrup sees in the homogeneous zone, a rotary motion which tends to keep the waters near its centre close to the coast. This analysis is an advance on earlier thought since it labels more precisely those masses that spread westward over the ocean, and those which are retained in eddy.

The eddy is of course in vertical plane and is considered by Prof. Sverdrup to be a barrier to transport westwards unless the eddy widens by recruiting water from below. In consequence of this inhibitory effect Prof. Sverdrup claims for it the property of a coast line and states that it will give rise to a modified upwelling in the open sea. Such a movement is noted as having been observed on the third cruise on 26—27. June.

On the majority of coasts, the circulation is not so simple as the conditions are here made out to be and the reader may be forgiven for demanding more extensive observations. On the west coast of South America for instance, where many more observations have been made, a series of countercurrents and of horizontal eddies make it impossible to assume uniform velocities parallel to the coast. Upwelling also varies greatly from day to day and with it the structure and proportions of vertical eddies; so that a variety of factors needs to be considered in estimating the transport of upwelled water and its influence on the open ocean. The value of the present paper lies not so much in elaborating these many factors as in attempting to reduce them to simple terms.

E. R. G.

S. W. Brujevicz and **E. S. Bruck.** "Determination of nitrates in fresh waters by the diphenylamine method." (in Russian). Journ. Applied Chem., Vol. 10, No. 12. Leningrad, 1937.

The diphenylamine method for the determination of nitrates in fresh waters is especially remarkable for its simplicity and rapidity and is thus applicable in the case of serial analyses. The authors of this paper have therefore found occasion to verify the use of the method under various experimental conditions.

Fresh waters differ from marine waters by very great fluctuations in their content of nitrate and by the presence of considerable amounts of compounds which may affect the results of the analytical method. This applies especially to organic substances, iron salts, and not infrequently to nitrates.

Investigations showed that for waters with a low nitrate content it is necessary to use one method with a corresponding reagent, the so-called D.F.A. reagent 15/1; while waters with more than 0·4 mg. nitrate N/l require another method and another reagent, viz., D.F.A. reagent 38/5 (see below).

For the analysis of waters with less than 0·4 mg. nitrate N/l, the standard solutions are as follows:— First, a solution is made up with 0·722 g. potassium nitrate in 1000 ml., and diluted 100 times, and an "initial standard" is obtained, containing 1 mg. nitrate N/l. From this a series of standard

solutions are made up in 100 ml. measuring glasses 0·00 — 0·5 — 1·0 — 1·5 — 2·0 — 3·0 — 4·0 — 6·0 — 8·0 — 10 — 15 — 20 — 30 and 40 ml. initial standard solution are pipetted off. To the glasses are added 5 ml. 20 % sodium chloride solution and 4 drops of sublimate solution, after which the tube is filled up with distilled water. The standard solutions thus prepared contain nitrate N in amounts of from 0·00 to 0·400 mg. per litre (small scale).

2 ml. of the standard solution are taken for the analysis, and 1·9 ml. of the sample of water, to which has been added 0·1 ml. 20 % sodium chloride solution. The standard solutions and the samples of water are transferred to clean, dry test-tubes of about 15 mm. diameter. To all the tubes 5 ml. D.F.A. reagent 15/1 are added with care, poured down the sides of the test-tube. After adding the reagent all the solutions are mixed as quickly and simultaneously as possible, while cooling in running water. The mixing is done with a special kind of stirrer; a glass tube with a ball blown at the end, having a diameter of 11—13 mm. The stirrer is moved up and down, the same stirrer being used for all the tubes without rinsing. The colorimetric comparison is made in the course of 2½ hours.

The D.F.A. reagent 15/1 is made up in the following way. 10 mg. diphenylamine are put into a 1000 ml. measuring glass with 150 ml. distilled water. Little by little the glass is filled almost to the top with concentrated sulphuric acid. After mixing and cooling the glass is filled right up with concentrated sulphuric acid.

Analyses of waters with a nitrate N content of from 0·4 to 5·0 mg/l. are made in a similar way.

A scale of standard solutions is made, containing 0·4—5·0 mg. nitrate N/l. To these standard solutions are added sodium chloride and sublimate as indicated under the "small scale" analyses. To 2 ml. of these standard solutions — 1·9 ml. water sample + 0·1 ml. 20 % sodium chloride solution — are added in the manner previously indicated 5 ml. diphenylamine reagent, but this time D.F.A. 38/5. The colorimetric comparison is made after 2½ hours.

The diphenylamine reagent 38/5 is composed of 50 mg. diphenylamine, 380 ml. distilled water, concentrated sulphuric acid up to 1000 ml.

The sulphuric acid must be purified from any nitrate that may be present. This is done by boiling it for 15—20 minutes with 5 g. potassium chloride to 1 litre.

The addition of sodium chloride was originally suggested by T i l l m a n, who, however, only added 0·1 % sodium chloride, while the authors think that the addition of 1 % sodium chloride is an essential improvement.

The interdependency of nitrate contents is characterized by linearity.

If it is desired to determine nitrate in waters of quite unknown composition a provisional test may be made with D.F.A. reagent 38/5. This is added to the water sample in the amounts indicated above. If an intense blue colour appears very quickly, the sample contains more than 10 mg. nitrate N/l, and it will then be necessary before the final determination to dilute the water sample 10—20 times. If no colour appears in the course of an hour, the nitrate content is not higher than 0·4 mg./l. To facilitate a quick decision as to what reagent to use the following indications are given:

For river and lake water in the summer: D.F.A. 15/1.
For river and lake water in the winter: DF.A. reagent 38/5.
For water from non-polluted artesian wells: 15/1.
For water from wells: 38/5.

Polluted water from wells should be diluted before analysis.

Various factors are of importance for the correctness of the analytical results:

1. The natural colour of the water sample.
2. The content of nitrate.
3. The content of iron.

The influence of the natural colour of the water on the correctness of the analytical results is not so great that it is necessary, in the case of water with a colour intensity of less than 200° according to the platinum-cobalt scale, to subject the water sample to a coagulation, particularly since the latter, in the case of waters poor in nitrate, will itself give rise to errors.

With a diphenylamine reagent *nitrite* gives the same reaction as nitrate. The result of the analysis will, then, be too high on determining nitrate in nitrite-containing waters. It will therefore be necessary to eliminate the nitrite from the water sample, which may be done as follows. To 10 ml. of water are added 20 mg. urea and a drop of concentrated hydrochloric acid. The mixture is allowed to stand over night, by which procedure the nitrite will be separated quantitatively.

It is more difficult to determine the nitrate content of waters containing iron (the iron is found in solution as ferro-iron). On adding the diphenylamine reagent the sample is coloured grey instead of blue, which will of course render the colorimetric comparison difficult. The iron can be removed by coagulation with aluminium sulphate; but since the coagulation process itself considerably reduces the analytical result, this method can only be adopted for waters with so high a content of iron that the influence of the iron is greater than that of the coagulation under the conditions at hand.

The analytical method may be simplified considerably by the use of photometry or by employing a permanent colour scale. The latter is made up of solutions of indigo carmine and cobalt sulphate kept handy, but it must be checked by solutions with a known content of nitrate to which D.F.A. reagent has been added. The comparison is made after 2½ hours. A permanent colour scale made in this way will keep for some days in the summer, and for a long time in the winter.

Table 4 of the paper contains 4 columns. Column 2 indicates the amount of 1 % indigo carmine solution, Column 3 the amount of cobalt sulphate 10 %, Column 4 the amount of distilled water to be mixed to obtain a solution with colour intensities corresponding to the amounts of nitrate given in Column 1.

Curiously enough, the authors have made no attempt to eliminate the chief sources of error in the analytical method discussed, viz. the natural colour of the water and the iron content of the water. The natural colour of the water might be eliminated by using compensation filters in the colorimetric comparison. The iron content of the water might perhaps be eliminated by oxygenation in a basic liquid or merely by aerating followed by filtration.

H. Baggesgaard Rasmussen and V. Sten Andersen.

A. V. Trofimof. "Photometric study of the diphenylamine reaction for the determination of small quantities of nitrates in water." (in Russian). Journ. Applied Chem., Vol. 9, No. 4. Leningrad, 1935.

The author refers to the Grandvalja-Ljaschu picrate method commonly used in Russia, but the method is not applicable to present

purposes. Amongst other defects it is particularly sensitive to chlorides. The author therefore adopted the diphenylamine method proposed by T i l l m a n and others.

The paper explains the chemical process in the diphenylamine reaction as applied to waters containing nitrate, under many different experimental conditions.

The formation of the blue-coloured compound by the influence of nitrates on diphenylamine is associated with an oxidation of the latter. The same reaction is obtained by the influence of a number of other oxidation agents such as nitrate, chlorate, perchlorate, bromate, iodate, chromate etc. The sensitivity of the reagent of course differs with the different oxidation agents. It attains its highest sensitivity to nitrate in a strong sulphuric acid liquid in the presence of chloride. This would seem to indicate that it is not the nitrate itself which has an oxidizing effect, but the chlorine and nitrocyl chloride formed by the nitric and hydrochlorine acids.

$$HNO_3 + 3HCl \rightarrow 2H_2O + NOCl + Cl_2.$$
$$NOCl + H_20 \rightarrow HNO_2 + HCl.$$

The formation of the bluish-violet colour substance takes place as follows:—

Oxidation: $2\ (C_6H_5)_2NH + O \rightarrow H_2O + (C_6H_5)_2NN\ (C_6H_5)\ 2.$

Redeposition: $(C_6H_5)_2NN(C_6H_5)_2 \rightarrow C_6H_5NHC_6H_4C_6H_4NHC_6H_5$ (Diphenylbenzidine).

Oxidation:

$$(C_6H_5NHC_6H_4)_2 + H_2SO_4 \rightarrow C_6H_5NHC_6H_4C_6H_4NHC_6H_5OSO_3H + H_2.$$

The colour substance thus formed, which must be supposed to be the final product of the reaction, is only stable in a strong sulphuric acid liquid, and is not stable in excess of diphenylbenzidine, which together with the colour substance gives a polychinoid compound of the kinhydron type of a yellowish green colour. The velocity of the formation of the yellowish green colour substance is proportional to the excess of diphenylbenzidine, and this surplus is again dependent on the amount of diphenylamine added.

If it is desired to attain the greatest possible stability of the bluish-violet colour, it will be necessary to see that such conditions are present as accelerate the formation of this and prevent the transformation to the yellowish-green compound, that is to say, a high concentration of sulphuric acid and a low excess of diphenylamine.

As previously mentioned, the colour reaction, apart from the influence of chlorides, is dependent on the amount of diphenylamine and on the concentration of sulphuric acid, as also, of course, on the amount of nitrate in the water sample in question.

It may also be expressed as follows. The smaller the ratio diphenylamine/nitrate, and the greater the ratio sulphuric acid/water, the better are the conditions for the development of the bluish-violet colour.

The ratio of the sulphuric acid to the water is fixed by the investigator himself, while the ratio between the diphenylamine and nitrate differs for the different water samples.

Experiments have shown that the colour attains its maximal intensity in a solution containing 74 % weight percentage of sulphuric acid, when the molar ratio between diphenylamine and nitrate is 110, while the maximum of colour intensity is attained more rapidly with higher concentrations of diphenylamine and more slowly with lower concentrations.

For example:—

The ratio diphenylamine/nitrate 11 — max. 49 colour units after 15 hours.
" " 110 — max. 180 " " " 10 "
" " 1100 — max. 40 " " " 2 "

From the particulars given in the paper it follows that to attain the highest colour intensity at very low nitrate concentrations (0—10 mg. nitrate N/m.^{3}), a diphenylamine concentration of 2—5 mg. per litre must be employed. Nevertheless the very slow development of the colour at low diphenylamine concentrations compels the analyst to use a higher concentration of diphenylamine in the reagent.

For waters with 0—100 mg. nitrate N per m.^{3} a reagent consisting of 10 mg. diphenylamine in 1 litre of sulphuric acid (d = 1·81) may also be successfully employed. This reagent, in the course of 2—3 hours after mixing, yields colour intensities proportional to the nitrate content of the water sample.

As already mentioned, it is necessary for the development of the bluish-violet tint that there should be a content of chlorides in water samples for nitrate determination by the above-mentioned method. This necessitates the addition of sodium chloride to water samples devoid of chloride, and to the standard solutions used for the colorimetric comparison.

Experiments show that an increase of the chloride content from 0 to 1 $^0/_{00}$ causes a great increase in the colour intensity, while an increase from 1 to 10 $^0/_{00}$ does not have a proportional effect, and finally, that a chloride content of more than 10 $^0/_{00}$ sodium chloride causes a weakening of the colour.

It is not only necessary, therefore, to add sodium chloride to waters poor in chloride, but it is also necessary to reduce the chloride content of waters with more than 10 $^0/_{00}$ NaCl; this is done by boiling with sulphuric acid. This metod for the elimination of clorides has been verified by experiment.

It has been shown by experiment that the above-mentioned effect of chlorides is specific, other electrolytes that generally occur in marine waters having no effect whatsoever on the reaction. This also applies to sublimate in small amounts, which may therefore be used for the conservation of water samples.

If the reaction is carried out with the same nitrate solution under otherwise equal conditions, but at different temperatures, for instance at 0° and at 20°, at 20° the maximum colour intensity is attained after 5—6 hours, and the solution will be completely decoloured after 20 hours. If, on the other hand, the work is done at 0°, the colour does not attain its maximum intensity for the first 20 hours. The maximum obtained is higher than that at 20°. This shows that the higher temperature favours both the development of the bluish-violet colour and the conversion of the latter to the aforementioned yellowish-green colour. Since excess of diphenylamine, as mentioned above, likewise favours the rapid development of the bluish-violet colour and its dissolution, it is best to work at as low temperatures as possible with excess of diphenylamine.

The preparation of the diphenylamine reagent is as follows. To 1 litre of 89 $^0/_0$ sulphuric acid (specific weight 1·81) are added 5 ml. of a solution of 2 g. diphenylamine in 1 litre of sulphuric acid of the same concentration. If the finished reagent is quite colourless, it can be made more sensitive by adding quite a small amount of nitrate to colour it faintly.

If the sulphuric acid is polluted by nitrate this is removed by boiling with 5 $^0/_0$ KCl for 15—20 minutes.

Standard solutions are made from a solution containing 0·722 g. KNO_3 in a litre; it contains 100 mg. nitrate N/l. Standards: 0—10—20—30—40—60—100—150 mg. nitrate N/m.[3]

To these standards is added so much sodium chloride solution that they obtain a NaCl content of 1 %. The solutions are preserved with sublimate solution, 4 drops to 100 ml. of solution.

Exactly 2 ml. of the standard solutions and the water sample are transferred to clean, dry test-tubes. Down the sides of the tubes 5 ml. of reagent are carefully added. This settles at the bottom of the tubes. The contents of the tubes are then mixed as quickly as possible; it is important that the mixing should be done as quickly and as simultaneously as possible (as to the technique, see the review on the determination of nitrate in fresh water p. 280). During the mixing the tubes are placed in running water so as to avoid too much heating. The colorimetric comparison is made after ½—3—4—6 hours according to the temperature and the nitrate concentration.

The error of this analytical method is about 5—10 % for nitrate concentrations of more than 20 mg. nitrate N/m.[3]; for lower concentrations the error is greater.

A very simple apparatus may be used for these measurements, consisting of a source of light and a photo-electric cell connected to a galvanometer.

The untreated water sample is first placed in a cuvette which is put between the source of light and the cell, and the deflection i_0 of the galvanometer is read; then the water sample treated with diphenylamine reagent is transferred to the cuvette and the deflection i of the galvanometer is read.

Introducing the numerical values for the two readings into the formula

$$\log i_0 - \log i = C, \text{ or } C = \log \frac{i_0}{i}$$

we have in the numerical value of C a measurement of the colour intensity of the solution, and thus also of the nitrate content of the water sample.

This method has the great advantage that C may be calculated once and for all for a series of nitrate solutions with a known nitrate content. If the results are plotted, it is merely necessary in later determinations to measure i and i_0, calculate C, and then to read the nitrate content N of the water sample from the curve.

H. Baggesgaard Rasmussen and V. Sten Andersen.

S. W. Brujevicz and **E. I. Pletnikova.** "Determination of phosphates in cloudy and coloured natural waters." (in Russian). Journ. Applied Chem., Vol. 9, No. 5. Leningrad, 1935.

During the last decade the determination of biogenic elements has occupied a central position in the hydrochemistry of fresh and marine waters in connexion with the study of the production of organic substances therein.

In studying the various factors that condition the production of phytoplankton the determination of phosphates by the molybdenum blue method as evolved by Denigès has most commonly been used; but the apparent simpleness of the method often led to its uncritical use under highly different experimental conditions.

In researches carried out in the German Laboratory for Marine Research

K. Kalle demonstrated that colloid substances are nearly always found in fresh waters, a fact to which due consideration has not always been given in determinations.

Further, the ordinary method adopted to prepare the water for analysis, viz., filtering through paper filters and coagulation of the colloids by means of aluminium sulphate, is in some cases useless or at any rate inadequate. Atschnikofs gives some examples of the increase of dissolved phosphates in fresh waters, after filtering through filter paper, caused by small particles containing phosphate, which are able to pass through the ordinary paper filters.

For the purpose of eliminating the influence of the precipitate and the natural colour of the water in the determination of phosphates the authors of this paper introduce the following improvements and examine them critically:

1. Filtering through membrane filters.
2. Coagulation of waters containing colloids by means of barium chloride and sulphuric acid.
3. The use of colour filters for the elimination of the natural colour of the water.

The method adopted for the determination of phosphates is in all essentials the same as that accepted at the Oceanographic Conference in Oslo in 1928.

To 100 ml. of the water sample is added 2 ml. ammonium molybdate reagent (250 ml. 10 % ammonium molybdate solution + 750 ml. 50 vol. % sulphuric acid); it is then cooled under the tap, and two drops of stanno-chloride solution are added. The stanno-chloride solution is made up as follows:— 25 mg. tinfoil are dissolved in 2 ml. concentrated hydrochloric acid and made up with distilled water to 10 ml. The sample is allowed to stand for the development of full colour intensy (about 5 minutes), when the comparison is made with standard solutions of known phosphate content made in a similar way.

For filtration of natural waters for phosphate determination the investigator uses membrane ultra-filters of nitrocellulose, these filters having the advantage over paper filters that they are able to retain even the finest particles.

It is pointed out that it is necessary to filter twice, both before and after the coagulation mentioned later. If the investigators filter after the coagulation only, the reagents used (the acid) will dissolve the particles containing phosphate (clay and mud) in the water, and the analysis will give too high a result.

The influence of colloidal humic substanges in natural waters was verified both with regard to the influence of the colour of the humic substances on the result of the colorimetric measurement, and with regard to the effect of these substances on the reaction itself.

The effect of the colour was eliminated by using a compensation colour scale. This scale consists of glass plates of a yellow colour, corresponding to the colour of the water sample under consideration, measured by the platinum-cobalt scale. The glass plates are placed under the colorimeter glasses with the standard solutions. Experiments with phosphate solutions coloured with burnt sugar free from phosphate showed that the effect of the colour itself could be eliminated by the use of the colour filters mentioned in the case of waters with a natural colour of from 5° to 40°

measured by the platinum-cobalt scale, if the phosphate content of these waters did not exceed 0·100 mg./l.

In order to ascertain the effect of the humic substances on the colour reaction itself phosphate determinations were made on solutions with a known phosphate content, to which had been added humic acid of colour intensities up to 30—50°.

The author shows that coagulation of coloured waters with aluminium sulphate gives too low a result in the phosphate determinations, perhaps because the phosphates are precipitated together with the precipitated aluminium hydroxide.

The method described below resulted from a series of coagulation experiments.

To 200 ml. of water sample is added 1 ml. of 8 % sulphuric acid (4·4 ml. sulphuric acid of specific gravity 1·84 in 100 ml. of water), and 1 ml. 10 % barium chloride solution. After 2 hours the precipitated sediment is filtered off through one of the above-mentioned filters. By this method the colour intensity of waters with a natural colour of 25—50° is reduced by about one-half. If compensation filters are used, the remaining colour allows of sufficient accuracy in the determination of phosphates.

As an example of the great effect which the acid used in the coagulation process may have on the phosphate determination in cloudy, non-filtered waters, the author describes some investigations on the phosphate content of turbid river water before and after filtering. These investigations prove that it is possible to make a determination of dissolved as well as undissolved phosphates in cloudy and turbid natural waters, which is of the greatest importance for the investigation of the balance between dissolved and undissolved phosphates in these waters.

H. Baggesgaard Rasmussen and V. Sten Andersen.

S. A. Waksman, J. L. Stokes and **M. R. Butler.** "Relation of bacteria to diatoms in sea water." Journ. Mar. Biol. Assoc., Vol. XXII, No. 1, pp. 359—373. Cambridge, 1937.

Zur Untersuchung über die Funktion der beiden Hauptgruppen des Phytoplanktons, nämlich der Diatomeen und der Bakterien, die sich einander im marinen Lebenszyklus ergänzen, wurden folgende vier Methoden, die hier nicht näher referiert seien, angewandt: 1. Sauerstoffverbrauch durch Diatomeenmaterial, mit dem das Meerwasser angereichert war. 2. Stickstoffbildung im Meerwasser als Ergebnis bakterieller Tätigkeit. 3. Rückbildung von Phosphor. 4. Bakterienwachstum (Plattenmethode). Filtriertes Seewasser wurde mit isoliertem Phytoplankton (lebenden und toten Diatomeen) und mit gemischtem Plankton (Diatomeen *und* Zooplankton) angereichert und zwar in einer Konzentration, die ungefähr der der natürlichen entspricht. Die Kulturgefässe wurden im Hellen resp. Dunkeln aufgestellt.

Es wurde gefunden, dass *tote Diatomeen* sofort von Bakterien abgebaut werden und einer raschen Oxydation unterliegen, wenn man sie in frisches Seewasser bringt. Bei Vorhandensein zusätzlicher Energiequellen (Glucose) kann das beim Abbauprozess freigewordene Phosphat für die Vermehrung der Bakterien verwendet werden. Zu Beginn des Abbauprozesses erfolgt gewöhnlich eine Abnahme des gelösten Phosphates. Die Abnahme wird durch raschen Aufbrauch durch die sich anfangs stark vermehrenden Bakterien erklärt. Nachdem das Maximum der Bakterienzahl in kurzer Zeit erreicht

ist, fällt sie rasch auf ein nahezu konstantes Minimum herab. Mit der Selbstzersetzung der Bakterien wird das Phosphat wieder an das Seewasser abgegeben. Im Verlauf von 132 Stunden wurden durch die Wirkung dieses Phosphorzyklus im Seewasser $^2/_3$ des in den Diatomeen vorhandenen Phosphors festgestellt.

Bei *lebenden Diatomeen,* die in frisches Seewasser gebracht und im Dunkeln aufbewahrt wurden, schritt der Sauerstoffverbrauch fort. Sie wurden von den Bakterien des Seewassers nicht angegriffen. Sie besitzen also selbst bei Fortfall einer Photosynthese ein beträchtliches Widerstandsvermögen gegen Bakterienangriffe.

Wurde dem Seewasser eine geeignete abbaubare organische Substanz z. B. Glucose zugesetzt, so war der Bakterienanwuchs weit grösser als in Seewasser, das mit lebenden Diatomeen angereichert war.

Beim Abbau *diatomeenreichen Planktons* ist ein solcher Parallelismus wie im ersten Versuch nicht vorhanden, da für den Abbau auch die im Plankton vorhandenen Copepoden und Infusorien verantwortlich zu machen sind. Im letzten Falle wurde Stickstoff nur in geringen Mengen freigemacht und die Bakterienzahl wuchs in einem nur begrenzten Ausmasse im Vergleich ihrer Zahl im freien Wasser.

Wenn Seewasser, in welchem eine Photosynthese in wechselnden Zeitperioden fortschreiten konnte, plötzlich dunkel gestellt wurde, erfolgte eine rasche Oxydation des frischsynthetisierten Materiales, wie es der Sauerstoffverbrauch und das Freiwerden von Phosphor und die Phosphatenentwicklung anzeigte. Obgleich eine grössere Anzahl Bakterien in dem Wasser, in welchem eine Photosynthese stattgefunden hatte, vorhanden war, war die Oxydation frisch aufgebauten Diatomeenmaterials nicht von einem grösseren Bakterienwachstum begleitet; es war sogar häufig eine Verminderung der Bakterienzahl beobachtet worden. Wurde die Photosynthese durch Aufbewahren der Kulturflaschen im Dunkeln unterbrochen, so erfolgte eine auffallende Zunahme in der Protozoenzahl, wie Amoeben, Ciliaten und auch Copepoden.

Die Versuchsergebnisse lassen vermuten, dass für den Abbau lebender Diatomeen im Plankton in grossem Masse tierische Formen verantwortlich zu machen sind. Die Polle der Bakterien bei der Stickstoff- und Phosphatbildung besteht in der Zersetzung abgestorbener Diatomeen sowohl, als auch in der Zersetzung tierischer Zerfalls- und Abbauprodukte.

Helmut Schach.

J. Furnestin. "Influence de la salinité sur la répartition du genre *Sagitta* dans l'Atlantique Nord-est." Rev. Trav. de l'Office des Pêches Maritimes. T.XI, Fasc. 3. Paris, 1938.

Since F. S. Russell discussed the relationship of *Sagitta elegans* and *S. setosa* in the English Channel with the to-and-fro movements of Atlantic water at its entrance the significance of the various species of *Sagitta* as indicators is being more and more fully realized. Furnestin, in this paper, deals with the distribution of three species in the waters surrounding the British Isles — *S. setosa, S. elegans* and *S. serratodentata.* The agreement in so far as his stations overlap those taken by the Scottish vessel "Explorer" is gratifying but it is unfortunately limited to July, August, and September 1936. He shows that the distribution of these three species is associated with salinity. *S. setosa* was found in waters of less than 35 $^0/_{00}$ in the southern North Sea, eastern English Channel, Irish Sea south of the Isle of Man, and

off the south coast of Ireland, and also in places such as the surface waters of the Gulf of Gascogne where the entrance of river water from the Gironde sufficiently affects the otherwise high salinity. *S. elegans* is chiefly confined to water of more than 35 $^0/_{00}$ but strays into neighbouring masses of less saline waters to a small extent. *S. serratodentata* is very rare in water less than 35 $^0/_{00}$ and is to be found most commonly in water of 35·30 $^0/_{00}$ and over. This relationship is shown to be true for both geographical and vertical distribution. In areas where two or all three species occur together the *S. setosa* is to be found near the surface in water less saline than 35 $^0/_{00}$ and *S. elegans* below in water more than 35 $^0/_{00}$. *S. serratodentata* may be found if the sub-surface salinity is high enough (though, incidentally, it is a surface form in purer Atlantic water).

Although it is stated that *S. serratodentata* is a more truly Atlantic species than *S. elegans* it is not made clear enough that *S. elegans* is almost absent in the purer Atlantic water and is therefore an indicator of a mixture of Atlantic and coastal waters. Furnestin is in error when he assumes that areas of low salinity water and *S. setosa* extend northwards at the surface on both the Norwegian and Scottish sides of the North Sea, for although the general swirl of the North Sea currents, together with the Baltic influence, makes conditions suitable for *S. setosa* on the continental side, the water off the whole east Scottish coast is typically inhabited by great concentrations of *S. elegans*. This error is probably due to basing too much on a short survey. Temperature is shown to be of little or no significance in the distribution of these three forms.

The limits of distribution of these species, particularly between *S. setosa* and *S. elegans*, are reduced to almost superfine degree of salinity, which, together with the logical deductions are somewhat over-stressed. Furnestin has the basis of a future and very valuable paper indeed in the elaboration of his final paragraph "Ces renseignments présenteront un certain intérêt, dans les régions comme l'entrée de la Manche ou la Mer du Nord, par exemple, où des masses d'eau de salinité différente se trouvent brusquement en contact, et à la limite desquelles s'installent souvent les bancs de poissons (Maquereaux dans les eaux atlantiques, Harengs dans les eaux continentales), que nos bateaux de pêche recherchent, souvent à l'aveuglette."

J. H. F.

R. Gurney. "Larvae of Decapod Crustacea. Part V. Nephropsidea and Thalassinidea". Discovery Rep., Vol. XIII, pp. 291—344, 39 figs. Cambridge, 1938.

The latest report on the "Discovery" decapod larvae deals with a particularly interesting group. Little is known concerning the life histories of the Thalassinidea, for hitherto only isolated instances have been worked out and information is very scattered. The material dealt with is large, including, besides the "Discovery" collections, larvae from Mr. F. S. Russell's Barrier Reef plankton and samples from Samoa taken by Professor Buxton. By bringing all this together for comparison the work is made trebly valuable.

The larval Thalassinids from these collections belong mainly to the group here called the Axiid-Callianassid group. It is impossible with our present

imperfect knowledge of adults to be certain whether they are Axiids or Callianassids, the characters overlapping to a remarkable degree. It has been found possible, however, to place them in an ordered scheme which brings out the important relationships and, for the most part, to prophesy, with a good deal of probability, as to which are Axiids and which Callianassids. The work has entailed a large amount of labour, fully justified, for it has most certainly advanced our knowledge of these forms and cleared the way for other workers. The writer of this review, at present working in Bermuda, has found these schemes of great value in trying to place the new and little-known larvae in this area, a large number of which are noted for the first time in this report. There are many more of these larval forms than there are known species to fit them, and there must be numbers of adults yet to be found and described. Their habitat is almost certainly a difficult one in which to collect and it will be long before all the gaps are filled. Meanwhile we are given these groupings, and the subgroupings may prove to correspond to valid systematic divisions.

On the whole, the variety in the Axiid-Callianassid group is very large and in startling contrast to the larvae of the Upogebiidea as here restricted, which for the main part are uniform in structure, only two being found to deviate much from the typical form, one of which has an abbreviated metamorphosis unusual in the family. In the Laomediidae a *Jaxea* larva and a *Naushonia* (?) larva are described, both showing affinities with the Upogebiidae and differing widely from the Axiid-Callianassa type. Included in the report are two larvae which prove to be closely related to the Axiidae; one of these, from the Barrier Reef, is a species of *Nephrops* which is almost certainly a link between the Nephropsidea and the Axiidea, whilst the second, *Enoplometopus* sp., from the "Discovery" collections, is now actually assigned to the Axiidea.

The view, previously put forward by Gurney, that the Axiids and Callianassids form a homogeneous group as opposed to the Upogebiidea and Laomediidea is here strikingly upheld and one is in complete agreement with the suggestion that the Callianassids should be definitely removed from the Upogebiidea, the first to be placed near the Axiids, the second near the Laomediidea. It is shown that the adults also will bear this separation, which appears to be a perfectly natural one. We thus have the Axiidea and the Callianassidea with homarine affinities as opposed to the Upogebiidea and Laomediidea, which have mainly anomuran characters.

M. V. L.

1. **W. J. Dakin.** "The habits and life-history of a Penaeid Prawn (*Penaeus plebejus* Hesse)." Proc. Zool. Soc. London, Ser. A, Vol. 108, Pt. 2, pp. 163—183, pls. i—vii. London, 1938.

2. **J. H. Heldt.** "La reproduction chez les Crustacés Décapodes de la famille des Pénéides." Ann. Inst. Oceanogr. Monaco, N.S., T. XVIII, Fasc. 2, pp. 31—206, 131 text-figs. Paris, 1938.

The large prawns belonging to the family Penaeidae are the object of important fisheries on many tropical and sub-tropical coasts, and in the preserved state they are imported into Europe on a greater scale than is perhaps generally realized. It is surprising, therefore, to find how little information is available on their habits and life history. It has long been known that they have an extremely primitive type of larval development,

hatching from the egg in the form of a nauplius, but although the general characters of their larval stages are well known, the whole cycle has not been followed out in any single species. The most complete series of stages hitherto described was obtained at Suez by Dr. Robert Gurney and was believed by him to belong to *Peneopsis Stebbingi, Nobili.* It is a coincidence that the two important memoirs quoted above should have appeared within a few months of each other.

(1). Prof. Dakin has investigated *Penaeus plebejus,* Hesse, one of the two commonest species on the coast of New South Wales, where it is known as the King Prawn. It is fished in quantities in the estuaries and in coastal salt- or brackish-water lakes or lagoons. During the winter months the prawns are found only in the upper parts of the estuaries, even where the water is fresh, and are of small size. During the spring and early summer they move down towards the sea, growing rapidly, until in the late summer they go out to sea. Prof. Dakin gives a vivid description of this seaward migration as seen at the narrow entrance to Lake Illawarra, where each evening as it becomes dark the prawns suddenly appear in shoals heading for the open sea. "Their appearance is surprisingly abrupt and they may come in battalions". These prawns are of large size, 15—20 cm. in length, but their gonads are immature. Prawns of similar or even larger size, with well-developed gonads, are occasionally trawled at sea, but never, it seems, in large numbers. No larvae but only post-larval stages are found in the estuaries, but Penaeid larvae of various kinds are common in the plankton of the sea. Among these larvae Prof. Dakin was able, eventually, to piece together a series of stages leading up to a post-larval form that could be identified as belonging to the King Prawn. These larvae, of which the earliest was in a stage corresponding to Gurney's second Protozoea, are described and figured in detail. No nauplius stages were seen and Prof. Dakin was unable to decide whether the eggs (which in the Penaeids are not carried by the female as in most Decapods) are planktonic or demersal. Another unsolved problem concerns the fate of the adults, whether they die after spawning or live on in the sea to breed more than once. It is certain that they do not return to the estuaries. The breeding season is believed, from the occurrence of larvae, to extend from January to August, with a maximum in March and April. Prof. Dakin estimates that at least 18 months are required for the completion of the life cycle.

(2) Madame Heldt's researches were carried out at the Marine Station of Salambô in Tunis. Here she was able to study five out of the twelve species of Penaeidae known to occur in the Mediterranean. The complete life history from the egg to the adult condition was worked out in *Penaeus trisulcatus,* Leach, and *Sicyonia carinata* (Olivi), and the greater part of it in *Parapenaeus longirostris* (Lucas), *Gennadas elegans,* S. I. Smith, and *Solenocera membranacea* (H. Milne-Edwards). For the first three of these species it was possible to observe the deposition of the eggs and the hatching of the nauplius in captivity, and for *Penaeus* and *Sicyonia* the complete series of stages was reared in the laboratory, a task that must have demanded unusual patience and skill. In *Parapenaeus,* where the rearing of the larvae presented special difficulties, the larval life appeared to be greatly prolonged, and Mme Heldt mentions the possibility that this, and the large number of moults passed through, may have been due to the unfavourable conditions in the laboratory. In *Penaeus* and *Sicyonia,* however, every stage reared could be matched with larvae caught in the sea.

In *Penaeus,* the largest and economically the most important of the

species dealt with, the life history may be outlined as follows. The prawns are found in the brackish water of estuaries and in lagoons where the salinity may be less or greater than that of the sea. Apparently only immature individuals up to 7 cm. long are found in these localities and in the autumn (August to October) they migrate to the sea, much in the way described for the Australian species by Prof. D a k i n. During the winter few specimens are seen, but in the spring and throughout the summer they congregate on certain spawning grounds where quantities of very large individuals (up to 20 cm. in length) are taken by the trawl.

The process of copulation was not observed, and although the large and complex spermatophores were regularly found in the "thelycum" of females the method of fertilization remains something of a mystery. The eggs when deposited are enveloped in a jelly-like substance (not found in the other species studied) which caused them to adhere to the bottom of the container when oviposition was observed in the laboratory. The number of eggs deposited by a single female was estimated at over a million.

The nauplius larvae are poor swimmers, not rising far from the bottom, and they were only captured at sea when townets were attached to the frame of the dredge. There are eight nauplius stages, followed by three protozoea stages found in the mid-water plankton. The four mysis stages following are the most active of all and are found in the plankton at various depths. The four succeeding stages are distinguished as "post-mysis", less active swimmers which, however, are still planktonic and appear to accomplish the migration towards the coast. The post-larval stages are found on the bottom in very shallow water and undergo eleven moults, in the course of which they gradually assume the characters of the immature adult.

Mme H e l d t does not consider that the adult prawns die after breeding, since females that spawned in the laboratory appeared quite vigorous and continued to live normally.

The various larval and post-larval stages of the species studied are fully described and abundantly and excellently illustrated. Mme H e l d t is to be congratulated on this fine memoir, which is of the greatest interest to the zoologist as well as to the student of fisheries. Nor must we omit to mention her little son R o b e r t, who, at a very tender age, shows promise of becoming an observant marine naturalist.

W. T. Calman.

A. Bollmann. "Die Chätognathen der Deutschen Antarktischen Expedition auf der 'Deutschland' 1911/12". Internat. Rev. d. ges. Hydrobiol. u. Hydrogr., Bd. 30, H. 3/4, S. 251—305, 9 Textabb., 2 Taf., 3 Tab. Leipzig, 1934.

This paper is an account of the Chaetognatha taken by the "Deutschland" during her outward passage from Europe to the Antarctic in the summer and autumn of 1911, and during the winter of 1912, when for a time she was beset in the pack-ice of the Weddell Sea. The "Deutschland"s Atlantic observations extended from the English Channel southwards to the Falkland current, those in the Weddell Sea from about 73° S. to about 64° S.

The bulk of the work is concerned with a quantitative study of the horizontal and vertical distribution of the Chaetognath population in the Atlantic Ocean and Weddell Sea; but perhaps the most important part is

that dealing with the vertical distribution of certain of the more commonly occurring Atlantic and Antarctic species. Of particular interest in this respect is the attempt to fix definitely the various depth levels at which the species in question occur in greatest abundance. Here, although working under somewhat unfavourable conditions, since the "Deutschland" employed for the most part only open nets, the author achieves a considerable measure of success, his results for certain species (notably *Sagitta decipiens*) showing a close general agreement with a large body of as yet unpublished evidence accumulated on this question in recent years by the vessels of the "Discovery" Committee. On the whole, however, it is felt that figures and conclusions based on the catches of open nets should be accepted with some reserve.

As to the species themselves the majority of the already known Atlantic and Antarctic Chaetognatha are recorded. It is strange, however, that there is no mention of *Sagitta robusta*, a very distinctive, and by no means rare, tropical Atlantic form. The author, moreover, appears to have had difficulty in distinguishing satisfactorily between *Sagitta lyra* and *Sagitta gazellae*, and between *Eukrohnia hamata* and *Eukrohnia fowleri*, with the result that we are left in doubt as to the real distribution of these animals along the "Deutschland"s track both in the Atlantic Ocean and Weddell Sea. After all that has been written on the subject of *S. lyra* and *S. gazellae* (the latter a well-known Antarctic form) he apparently does not altogether exclude the possibility that both species may occur in the Weddell Sea. This matter should be cleared up once and for all. *S. lyra* does *not* occur in the Antarctic. It is a warm-water species, never, in the South Atlantic at least, extending farther south than 45° S. It is hardly less confusing to group *E. hamata* and *E. fowleri* together. The former, by far the most abundant of the Antarctic Chaetognatha, was naturally taken in large numbers by the "Deutschland" in the Weddell Sea, but although *E. fowleri* doubtless occurs there as well, just as it does in many other parts of the Antarctic, it does not necessarily follow that it may have been taken along with *E. hamata* in the "Deutschland"s Antarctic hauls as the author suggests. For *E. fowleri* is a species which in Antarctic seas lives at great depths, generally well below 1,000 m., and it could only have been taken by the "Deutschland" in the Weddell Sea provided her nets were worked down to the required level — which is not clearly stated.

The paper concludes with short systematic notes on twelve commonly occurring Atlantic and Antarctic species, illustrated by nine text-figures, mainly of Chaetognath heads. While the notes add nothing to Ritter Zahony's comprehensive *Revision der Chätognathen* of 1913 some of the figures may prove helpful to plankton workers when dealing with this rather difficult group.

J. W. S. M.

H. B. Bigelow. "Plankton of the Bermuda Oceanographic Expeditions. VIII. Medusae taken during the years 1929 and 1930." Zoologica, New York Zool. Soc., Vol. XXIII, Pt. 2, pp. 99—189, 23 figs. New York, 1938.

It is always with the greatest interest that one receives a paper on jellyfish by Professor Bigelow who, since 1904, has contributed so much to our knowledge of these delicate animals. The medusae are among the most beautiful organisms floating in the sea, and they are also particularly valuable as indicators of sea-currents. It is very useful, therefore, to have

the medusan fauna of a geographical area thoroughly worked up, from a systematic as well as from a distributional point of view, as has been done in the present case for a part of the Sargasso Sea south-south-east of the Bermuda Islands, above depths between 2480 and about 2700 m. More than 1000 horizontal hauls were made at various levels between the surface and depths of about 2000 m., and 33 species of medusae were secured. No new species were found, but in the case of several species this extensive material has enabled the author to add considerably to our knowledge of their morphology and to the classification and the limitation of species. The descriptions, some of which are accompanied by several drawings, will greatly facilitate exact specific determination in the future. Of special interest are the revisions of such much disputed genera as *Halicreas, Carybdea,* and *Atolla.*

The last five pages are devoted to faunistic and distributional considerations of considerable interest. As pointed out by the author, a comparison of the holoplanktonic species with the meroplanktonic, neritic, forms (the latter presumably all being derived from the coastal banks of the Bermudas) "gives a good indication of the extent to which a small isolated Bank may be expected to contribute to the medusan fauna of the open ocean nearby". Though among the 23 species of Hydromedusae 9 species were meroplanktonic (or may be assumed to be so), the number of specimens of this neritic element in the catches only amounts to 3 % of the total catch (17 out of 717 specimens). In the case of the Scyphomedusae the number of neritic specimens was considerably raised by two very large catches of *Linuche unguiculata* and *Carybdea xaymacana,* but apart from these the neritic (or probably neritic) Scyphomedusae numbered only 23 specimens to 549 specimens of holoplanktonic forms. As the collections were made by means of open nets hauled horizontally, exact calculations of the number of specimens at the various levels were impracticable. Nevertheless, by a calculation of the number of specimens per haul, and the percentage number of hauls containing medusae at various depths, the author has obtained some very interesting results, which may be summarized as follows. The neritic element among the Hydromedusae is numerically negligible; this also applies to the Scyphomedusae, except on occasions when swarms of one species or another may drift out for a few miles from the Bermuda Bank. The neritic species occur mainly in the surface water. The whole upper 500 m. of water are practically barren of medusae from spring, through summer, to autumn, except when such swarms appear; on these occasions, the immediate surface may be the most thickly populated zone. But it appears that these periods are of brief duration; nor is it likely that they affect the situation on a broad scale more than a few miles out from Bermuda. Medusae as a whole in this part of the ocean basin are usually most abundant and occur most regularly at about 500—800 m., below which they decrease with increasing depth.

A tabulation of the relative abundance of different species is also very interesting. Several species of Trachymedusae were fairly common, but among the Narcomedusae only one species, *Aeginura grimaldii,* was really abundant. The two bathypelagic Scyphomedusae, *Periphylla hyacinthina* and *Atolla wyvillei,* occurred in astonishingly great numbers. On the other hand, the genus *Liriope* among the Trachymedusae, which is widely distributed and frequently very abundant in warmer seas, was only represented by one individual in the numerous hauls in this part of the ocean.

A quantitative comparison of the medusa population of the Bermuda region with other regions show that the Mediterranean is many times the more productive region, both for the holoplanktonic Hydromedusae and for

the medusae as a whole. The Bermudian region is also poor in the holoplanktonic Hydromedusae as compared with the Central and South Atlantic, probably mainly on account of the barrenness of the upper 500 metres of water in holoplanktonic medusae of any sort, whereas the productivity of the deep waters in the more strictly bathypelagic forms, represented by *Periphylla* and *Atolla*, is more nearly of the same general order of magnitude in the Bermudian region, as it is over the ocean basins as a whole, or in the Mediterranean.

P. L. Kramp.

M. E. Thiel. "Naturgeschichte des Seemooses." Handb. Seefisch. Nordeuropas. Bd. III, H. 3, S. 1—34, Abb. 25. Herausg. von A. Willer. E. Schweizerbart'sche Verlagsbuchh., Stuttgart, 1938.

The first to use the elegant hydroids for decorative purposes was the Englishman J. Ellis; he was also the first to demonstrate, in the middle of the eighteenth century, the animal nature of these organisms. Towards the end of the nineteenth century and far into the twentieth, certain species of hydroids, particularly *Sertularia cupressina* and *Hydrallmania falcata*, constituted an important merchandise in Germany and also in Holland. They were dredged in great quantities in the south-eastern part of the North Sea with special appliances, and as late as in 1928 they brought the German fishermen an income of more than 100,000 R.M.; but after that time the yield of this fishery was much reduced (1400 R.M. in 1936). Formerly the hydroids, after cleaning, drying, and staining, were mainly used for decoration of lamps and other kinds of furniture; now they find some application as admixture to bouquets of flowers and, to a less degree, by architects and engineers for models of gardens.

This special fishery and the natural history of the hydroids in question have been thoroughly described previously by various German biologists, especially Eichelbaum (1912) and von Reitzenstein (1913), and now Dr. M. E. Thiel, of Hamburg, gives a modern survey of the matter. The methods of fishing and the preparation and application of the polyps are only briefly dealt with, whereas the author has given a very thorough description, not merely of the general appearance of the colonies, but also of the structure of the single individuals (nutritive and sexual polyps) in minute detail, illustrated by numerous excellent figures. Of particular interest is the biological section, with the demonstration of the practical importance of knowing the breeding-time, rate of growth etc., which must be considered in determining the most favourable season for the fishery (August to October) and for the significance of a protective season (the summer months). The maps accompanying the paper which show the localities where good hauls can be expected, and the tabular surveys of the varying annual yields in the period 1907 to 1936 are very interesting.

For anybody wanting information on the natural history of these pretty colonial animals, this treatise is very useful.

P. K.

D. D. John. "Crinoidea." Discovery Reports, Vol. 18, pp. 127—222, pl. III—VI. Cambridge, 1938.

Die umfangreiche Sammlung der Discovery-Crinoidea (326 Stück) stammt meist aus 100—600 Faden Tiefe aus der Antarktis, insbesondere dem südamerikanischen Abschnitt. Zwei Drittel davon gehören einer einzigen Art

an. 58 Larven wurden an den Cirren der Weibchen festsitzend gefunden. Es wurden 10 neue Arten und eine neue Gattung festgestellt. Die Zahl der lebendig gebärenden Formen erhöht sich von 3 auf 11, womit über 50 % der 19 bekannten antarktischen Arten lebendig gebärend sind. Bei allen diesen haben die Weibchen Bruttaschen neben dem Ovar. Ihrer Verbreitung und Verwandtschaft nach zeigen die antarktischen Arten Beziehungen hauptsächlich zur Ostküste, doch auch zur Westküste von Südamerika, wie das auch bei anderen Echinodermen der Fall ist. Erwachsene und Larven werden ausführlich beschrieben und es wird ein Bestimmungsschlüssel gegeben.

E. H.

M. V. Lebour. "Notes on the breeding of some lamellibranchs from Plymouth and their larvae." Journ. Mar. Biol. Assoc., Vol. XXIII, No. 1, pp. 119—144, 88 figs. Cambridge, 1938.

Von einer Anzahl Muschelarten werden Eier, Larven und postlarvale Stadien beschrieben. Das Material entstammt teils dem Plankton, wurde aber teilweise auch durch künstliche Befruchtung erzeugt und mit Flagellaten oder Diatomeen möglichst bis zur Erkennbarkeit der Art aufgezogen. Durch Untersuchung der Erwachsenen und des Larvengehalts im Plankton wurden die Brutperioden festgestellt. Eine grosse Anzahl Larvenarten tritt im Spätsommer und Herbst nach der zweiten Diatomeenwucherung auf, während im Frühling und Sommer oft eine einzelne Art vorherrscht. Die oft sehr zahlreich vorhandenen Larven haben grosse Bedeutung für die Ernährung anderer Planktonorganismen, u. a. junger Stadien von Hering und Sprott. Die frühesten Stadien der verschiedenen Arten sind kaum unterscheidbar, doch lassen sich die späteren oft an der Gestalt und Skulptur der Schale, der Lagerung der Organe, der Färbung u. dgl. erkennen.

E. H.

S. Kemp. "Oceanography and the Fluctuations in the Abundance of Marine Animals." British Assoc., Sect. D-Zool., pp. 85—101, 1938.

The subject of this lecture is the connexion between oceanography properly so called and its relation to marine life. The author refers to the great strides in our knowledge of marine physiology and natural history, made possible by the activities of various expeditions and by fishery research; he restricts himself however, to large-scale fluctuations noticed every now and then, and their possible causes. As these fluctuations are local, even in the same fish species, there must be an external influence that may foster or hamper the survival of the species in question.

The author cites the Plymouth herring fishery, in which the average weight per catch has declined deplorably in the last fourteen seasons, while at the same time the percentual age distribution of the stock reveals a marked decrease of the younger year-classes. This process has gone on until the fishery has become practically extinct. A similar phenomenon has been observed on the north coast of Donegal.

An explanation may lie in a notable change of the phosphate content in the offshore waters. As phosphates define the spring growth of phytoplankton it is to a great extent an indicator of the phytoplankton crop subsequently to be expected, and therefore also of the later abundance of zooplankton and fish larvae. Since 1931 there has been a marked deficiency

of phosphates off Plymouth, of which the author gives a table in which the connexion between the quantities of phosphates and fish larvae, expressed in certain standard quantities, is clearly shown. The decline is very remarkable indeed.

The Plymouth herring are winter spawners, so that at a period when plankton production is at a minimum the fish may normally still find the food they need in their full maturity. The reasonable assumption is therefore that these herring, while not appreciably hampered by lack of food, are nevertheless deflected from their usual paths of migration by the direct influence of "adverse" water. It seems, indeed, probable that the normal water movements off the mouth of the Channel have undergone a marked change in the last few years. This is corroborated by the decreased occurrence of certain plankton organisms of Atlantic origin. Useful indicators are three species of *Sagitta*, and it appears that one of these, *S. elegans*, typical of mixed Atlantic water, has greatly declined in numbers and has been superseded by *S. setosa*, an indicator of Channel water. So it seems definitely established that in the thirties the offshore waters near Plymouth have scarcely had any influx of mixed Atlantic water. This again is corroborated by the study of the residual current at the Varne Lightvessel, which Carruthers has shown to have taken a more northerly and less easterly course since 1931.

It is further stated that in 1915 and '16 a similar deficiency of phosphates occurred in the Channel, but relevant data on fish life in the Plymouth area are lacking on account of the war. It is worth mentioning that the process of decline of the fishery is not connected with changes in temperature and salinity, as patches of water of high salinity moved up the Channel in the period 1932—'34, and especially in 1933. It is only in the depleted phosphate supply that a correlation can be found. Obviously an influx of Atlantic water does not necessarily imply an improvement in the conditions of life of marine organisms. Its influence will depend on the amount of phosphates it carries, but the season in which the influx takes place is also of importance. The question arises of how far we have to deal with a periodic phenomenon. For a quarter of a century we have had some information about a counter-clockwise circulation of the water south of Ireland, reaching at times as far south as 48°30'N., but we are not in possession of observations which might show periodicity.

The author then discusses similar long-period fluctuations in fisheries. He cites the example of Norwegian cod fisheries off Bear Island, in which a considerable fall was observed in the period 1885—1924. Another instance is the cod fishery in Davis Strait, where in 1917, after a long period of deficiency, a revival set in. There is also the case of the herring on the Murman coast, where the catches in 1931—1933 were increasingly higher than in the ten preceding years. All these cases, to which numerous others might be added, point to the conclusion that the Arctic seas have become warmer (by presumably 1—2°) in the last few years, probably on account of the Atlantic drift becoming stronger.

These long-range fluctuations, whether they are accompanied by a change of phosphate content, a rise in temperature, or any other phenomenon, affecting fishes in one or another way, may influence other animals as well. Their cause is to be sought in oceanic waters of the open Atlantic. It is therefore essential that large-scale research should tackle the problem with this end in view. Despite international organization much remains to be done. The importance of such investigations is not everywhere realized;

indeed, nations are, as a rule, more occupied by their domestic problems, and it is very difficult to get co-operation in long-range observation that does not promise—as administrators are too prone to believe—immediate practical results. The resignation with which the author concludes that in the present state of international politics little can be expected in this way of research is nevertheless illuminated by a ray of hope that a time may come when, once the period of armament is over, attention will also be turned to the future of an industry which, without previous sowing and tilling, yields a great harvest.

J. J. T.

O. Sund. "Die Norwegische Seefischerei." Handb. der Seefischerei Nordeuropas, Bd. VIII, Heft 1a. Schweizerbart'sche Verlagsbuchh., Stuttgart, 1938. 181 S., 56 Taf., 211 Abb.

This instructive volume once more convinces us that no country in Europe (except Iceland) offers greater possibilities for sea fishing than Norway, whose waters, both in the fjords and farther afield, abound with fish. No wonder, then, that Norwegian fisheries occupy a greater proportion of the public care than anywhere else. Sea fisheries are not the main occupation of the nation; they rank third, and it is only from the Lofoten northwards that they come first. Even so, it is obvious that Norway, in her topographical and social structure, is more dependent on the ocean than any other European country. From the very beginning of this volume instructive tables make us realize the very great importance of the sea fisheries to this country. This impression is still more forcibly brought to mind by the author's own method of graphical representation of statistical material by symbols, all around the intricate coast.

In the historical account of the development of the fisheries, we find descriptions and illustrations of the oldest types of fishing vessels, such as the famous Viking ships, "ottringer", "jesker", etc., all clinker-built and wholly or partly undecked. There follows a chapter on the fishing craft now in use: open boats propelled by oars, sail, or motor, or decked motor-vessels (cutters and "sköiter"), which latter are mostly small, averaging less than 50-foot long, engaged in line fishing or seining. Sea fishing is characterized by the absence of "capitalist" organization. Topographical and economic reasons have so far hampered the introduction of steam trawlers, as coal costs are high. Nevertheless, there are now more than 300 of such vessels registered, but as in 1936 the use of Norwegian ports and fishing in home waters was forbidden to trawlers, these vessels restrict themselves mostly to long-line and purse-seine fishing, transport of bait, towing etc. (From April 1939 a limited number of regular trawlers—provisionally 11 — is permitted but even this concession has caused considerable concern, as public opinion is much afraid of unemployment among fishermen). Nine trawlers fish off Bear Island and Spitsbergen and in the Barents Sea; their catch is salted.

The great variety of fishing implements is fostered by the complicated coast line and the multitude of small islands, which provide ideal shelter for occasional and professional fishing. Chief among the fishing methods are hand- and long-lines, Danish seine, baskets, traps, drift-nets, with, above all, the various kinds of seines, "nöter", "landnot, stengenot, snurpenot". These are as characteristically Norwegian as the peculiar wooden buildings ("rorboder") scattered along the coast, mostly in the Lofoten area, and used

for storing nets and gear, as well as temporary lodgings for the fishermen. Then there are the numerous scaffoldings (or simply flat places on the rocks) used for drying fresh or salted roundfish; the many smoke and store houses, the canneries and factories for herring oil and meal, cod liver oil and manure —in all of which features Norwegian fishing industries have reached a perfection that bears witness to their great national importance.

The author then proceeds to consider the principal branches of the fishery, renowned over the world. The cod fishery may be differentiated in that for adult ("skrei") and for maturing cod ("lodde torsk"), the first in midwinter and early spring at the Lofoten, the second on the Finmark coast from April till June; the fish are caught by set nets, but more by lines. The Atlanto-Scandinavian herring ("fetsild, storsild, vaarsild") is the object of an enormous fishery all along the coast, especially from Cape Lindesnäs to Aalesund. Only fetsild and smaasild are more particularly caught north of Trondheimsfjord; fishing is done by set nets, drift-nets, land- and stengenot, especially the snurpenot (in later years), helped by searchlights. The sprat may be a small fish, not much appreciated in other countries on account of its irregular appearance and its admixture with young herrings, but in south-western Norway it is held in high esteem, as it has, since the 'eighties, given rise to the enormous canneries of Stavanger. By mutual agreement arrangements have been made for regulation and restriction of the sprat fisheries. This industry is carried on in summer in the fjords, with land- and snurpenot. Mackerel are fished in May and June, with drift-nets especially along the south coast, later on in the fjords with stream nets, trailing lines and purse seines.

Other fisheries of less importance along the coast are those for saithe, halibut, plaice and other flatfish, and salmonoids. In this connexion many interesting details are recorded; as, for instance, the finding of halibut in deep water (3—400 m.) in the Westfjord and elsewhere, where it is taken in nets, in lieu of the baited lines formerly used; the greatly increased catch of plaice by the introduction of the Danish seine; that of salmon and sea trout by means of bag or stake nets ("kilenöter" or "Lakseverp"), with false bottoms. Space allows only of a cursory glance at other small local fisheries for fjord cod, haddock, hake, Norwegian haddock, tunny, eel, lobster and prawn. Till lately the isolation of many fjords formed a serious impediment to the expansion of the activities of local fishermen, and their catch was mainly only intended for private use, but modern facilities have fostered the recent prawn (*Pandalus borealis*) fishery, and that for tunny. After trials with baited hooks and small harpoon guns, the best implement for catching tunnies appears to be a strong, specially constructed purse seine. Artificial culture of oysters in the polls, where the temperature of the surface layer in summer mostly exceeds 20°, is also capable of much development, but this belongs more to pisciculture than to free harvesting of the sea.

Norwegian fishermen do not confine themselves, however, to sheltered fjords and coastal waters. They fish herring and cod near Iceland, herring in the North Sea (here mackerel fishing with trailing lines has died out since the war years), cod on the banks of Helgeland and Möre; they go even as far as Davis Strait (parent ship, with dories) for halibut, and Spitsbergen. Herring are caught with drift-nets and purse seines; cod and halibut with long-lines. A shark fishery (for dogfish, ice shark, porbeagle and even basking shark) is carried on chiefly for the sake of the oil in the liver.

A further chapter is devoted to fishery products, their manufacture and sale. The importance of the sea fisheries may be gauged by the fact that

in 1935 the catch was more than 900.000 tons, with a value exceeding 77 million crowns. The chief exports are fresh and salt herrings, fresh and dried whitefish, canned brislings, herring meal and cod liver oil. Live fish, landed in cutters fitted with wells, are seen daily on the fish markets at Bergen and Oslo. It is obvious that preserved fish products play a most important part in export. Almost classical is the manufacture of stockfish, one of the earliest staple products and an object of barter in former times; klipfish is a relatively modern product.

The impetus of the present technical age is manifested by the erection of artificial drying sheds, store houses, cold storage, canneries etc. Small wonder that the authorities give their best attention to the diverse, sometimes conflicting, interests of so great a national industry. The fisheries are encouraged through legislation, registration, collection of statistics, care for the welfare of fisherfolk, facilitating the rapid spread of information, commercial treaties, control of fishery products, police survey, editing of sea charts. Scientific research is subsidized by the State to the extent of 10—20,000 crowns a year—and a capital sum of three million crowns has, since 1930, been set aside for investigations and trial of fishery methods. Thanks to this help there now exist many establishments for artificial fish culture, mostly for salmon, but also for cod and lobster (at Flödevigen) and for plaice (at Trondheim), and also oyster culture has till lately profited.

A private institution is "Selskabet til de Norske Fiskeriers Fremme", founded in 1879 at Bergen, to whose activities are due the founding of fishery museums; a weekly periodical, "Norsk Fiskeritidende", and a fishery calendar. Private organizations among fishermen have recently been amalgamated in one great union, "Norges Fiskarlag". The herring fishery and the trade in them are monopolized by the "Norges Sildesalgslag". Salvage, rescue work and the maintenance of life-boats are likewise privately organized.

The volume ends with a list of Norwegian fishes and other marine animals, with their vernacular and scientific names, and their value in 1929 and 1935. There is also a very useful list of explanations of Norwegian technical terms.

The great importance of the sea fisheries to a country where the wealth of the boreal fish fauna unfolds itself in all its economic grandeur justifies the bulk of a volume that is not only admirably written but also profusely illustrated.

J. J. T.

M. Graham. "Phytoplankton and the Herring. Pt. III. Distribution of Phosphate in 1934—1936." Min. Agric. & Fish., Fish. Invest., Ser. II, Vol. XVI, No. 3, pp. 1—26, 15 figs. London, 1938.

The intriguing problem of the apparent influence of phytoplankton upon the herring fisheries off eastern England continues to interest the staff of the Lowestoft Fisheries Laboratory. Phosphate determinations from the years 1934 to 1936 represent an important extension of the previous observations on hydrography and phytoplankton. The author intends to seek the background for the occurrence of the phytoplankton patches which may be so disadvantageous to a good herring fishery.

The 1934 observations on phytoplankton and phosphate distribution indicated that most of the surface waters in summer did not contain sufficient nutrient salts for the growth of *Rhizosolenia styliformis*. The South-West Dogger Bank Swirl was, however, provided with phosphate enough for the

maintenance of a large *Rhizosolenia* population, a "patch". A detailed discussion of the hydrographic conditions of the region north-west and south-east of the Dogger Bank leads the author to the conclusion that the swirl regularly receives its summer supply of nutrient salts from the northern part of the North Sea, where they accumulate under the thermocline.

The occurence of *Rhizosolenia* patches in the gateway between the coast and the Dogger Bank in 1933 was disastrous to the herring fishery. This seems to be due to the fact that dry weather reduced the outflow of fresh water from the Humber, so water from the northern North Sea was able to push through the gateway. This northern water was rich in phosphate and gave occasion to continued growth of the *Rhizosolenia* population. However, the occurrence of the patch is not determined by the strength of the outflow from the Humber only (that is, by the precipitation). Other factors may at times complicate the situation. The 1936 observations showed very little *Rhizosolenia*, probably on account of strong winds and much run-off from the land producing more unsettled hydrographic conditions. The success of a patch depends on the persistence of favourable conditions, including sunshine, supply of nutrient salts, and sufficient stability to keep the patch together. All these factors are favourable in weather associated with strong Atlantic influx, although the supply of nutrient salts does not directly originate in the Atlantic water; it seems to be accumulated locally in deeper parts of stratified North Sea waters.

Graham's observations corroborate those by Savage and Wimpenny on the phytoplankton, and seem to give a sound explanation of the common occurrence of *Rhizosolenia* patches at the south-west corner of the Dogger Bank. Further contributions on the phytoplankton-herring problem are eagerly looked forward to.

T. Braarud.

W. C. Smith. "The Manx Herring Shoals." Proc. and Trans. Liverpool Biol. Soc., Vol. LI, pp. 22—70, 14 figs. Liverpool, 1938.

The Manx herring fishery, which at one time engaged about 600 Manx vessels as well as boats from Cornwall and north Ireland, has shown a regrettable decline and is now carried on exclusively by boats from north Ireland and Scotland. The fishing grounds at the present time lie to the south-west of the island, which Smith divides into three zones — two inshore and one offshore — distinguished by characteristic differences in the size, age, and maturity of the herring which inhabit them. The inshore zones are adjacent to each other and extend from the Calf of Man to Peel, and from 4 to 8 miles off the coast. To the north of this region, in what is termed the northern inshore ground, the herring are small, modes occurring most frequently at 23 cm. and the majority of the fish having 2 or 3 rings on the scales. To the south, within the southern inshore ground, the shoals are characterized by larger and older herring. Fish with 3 and 4 rings normally predominate, while 26 cm. is the dominant modal size. The largest and oldest herring are found on the offshore ground, the most intensively fished area being within a radius of about 15 miles from the Chickens Rock, where the dominant age groups have 3, 4, or 5 winter rings. It is found that herring of the southern inshore and offshore areas are larger and mature earlier than herring of the same age from within the northern inshore grounds. Smith suggests that the apparent segregation of the shoals arises from differences in their spawning times, but a glance at a chart

of the areas in question shows that his data accord beautifully with the conception of segregation of a population of mixed age-classes according to their size and the depth of the grounds.

There is a scarcity of herring with more than 5 rings on the scales and the view is expressed, with very little supporting evidence, that the older fish become incorporated in the shoals of large Atlantic herring.

A little attention has been given to feeding and the amounts of abdominal fat. Abdominal fat increases very rapidly in June and reaches maximal values during the last week of that month. It is stated that the rapid increase in the fat values may arise from the arrival of a new class of herring, an explanation which does not take into account sufficiently the question of food abundance. Autumn spawning herring, which have been analysed so far, almost invariably reach their highest fat values towards the end of June or by the end of the first week of July, and according to the evidence submitted much more food is found in the stomachs of Manx herring in June than in any other month of the year.

While the report gives a clear account of some of the main features of the Manx herring shoals between 1923 and 1935, it suggests to the reader the need for a more comprehensive investigation in this region, including the precise location of the spawning grounds and the race characters of the spring and autumn spawners. There seems little doubt that the older autumn spawners come from the south, but confirmation is required. A study of the relationship between the Manx autumn spawning shoals and the Smalls herring and the herring which appear off Howth in June and July, in collaboration with other biological stations, would possibly throw some light on the migration of the Manx spawners and on the distribution of the herring with more than 5 rings on the scales.

Comparison between the numerous tables would have been facilitated if percentage figures had been used.

H. W.

O. Sund, G. Rollefsen and **J. Eggvin.** "Torsken og fiskehavet 1937." Fiskeridirek. Skr., Ser. Havunders., Bd. V, Nr. 7, S. 1—52, 29 figs. Bergen, 1938.

For several years Sund and his collaborators have published short annual reports on the main results of Norwegian research work on the Arcto-Norwegian stock of cod. The present paper gives (with a summary in English) a review of tagging experiments (Oscar Sund), the stock of cod 1937 (Oscar Sund), age analyses for cod (G. Rollefsen) and the oceanographic conditions in north Norway of special importance to the cod fisheries (Jens Eggvin). The many new and valuable results obtained show how well the Norwegian research work is planned and carried out.

Tagging of cod was carried out during the season 1936—37 in the Lofoten area and farther north; 1379 Cod were marked and liberated during 1937, of which 132 were recaptured in the same year. Most experiments gave fair results, though one yielded only about 2 % of recaptures, probably owing to the fish being caught in deep water (240 metres). The results confirm earlier experiments, but the experiments should give further information during the following seasons. It is worth noting that an experiment carried out on the Svendsgrund (north of Andenes) showed that fish marked there tend to keep to this area during the season, many following the submarine valleys which lead the stock to the coastal side of the

bank, i. e., into territorial waters. The migration southwards into deep water outside the coastal banks is mentioned, and Sund points out that the south-going current in the depths has a velocity of at least 9 km. per diem, which is nearly the same as the speed of the migrating cod. The study of the route followed by the migrating cod to the Lofoten spawning grounds, which is probably determined by this southgoing current in the depths, is a question of general interest in fish migration, and Sund's final results relating to this question will be of importance in the study of migration of cod in other areas also.

The several marking experiments carried out in recent years off Norway have provided much new knowledge regarding cod migration, the proportion of annual recaptures of cod, etc., and it would be valuable if all results were collected in a general survey.

In the next paper the stock of cod in 1937 is considered along the lines followed by Sund for several years. Cod were more plentiful than in 1936 but appeared especially in the more northern part of the "Skrei" area. Moreover, it was observed that the Finmark cod appeared at a distance from the coastal area, owing to the coast being blocked by warm water masses.

The age determinations by Rollefsen show interesting alterations within the stock of cod during 1936 and 1937; cod of a certain age in 1936 were about 8—9 cm. longer than in 1932, for instance, decreasing again in 1937 by about 2 cm. Rollefsen suggests that this is correlated with the amount of food available in northern waters (Østhavet); it might also have been worth while, however, to investigate the question in relation to the higher temperatures prevailing in the various nursery areas during recent years. As the spawning stock of Lofoten cod is composed of fish belonging to several populations from widespread areas (Spitzbergen, Bear Island, Barents Sea, Finmark, etc.), the question is difficult to attack; however, extensive tagging experiments in all waters from which cod migrate to Lofoten might give valuable results as to the origin of these components and the variation in size of the various age-classes gathering on the spawning grounds.

Rollefsen demonstrates that the average age of spawners in 1932—34 was 10½ years, in 1935—37, however only 8—9 years; this points to the cod having come, in the latter period, from an area with higher temperatures than those of the region in which the 1932—34 cod spent the period previous to their first spawning migration. It may be mentioned, incidentally, that variations in the size of the various age-groups of cod have been observed also in the Iceland-Greenland stock in recent years (Paul Hansen, Arni Fridriksson).

It is further stressed by Rollefsen that the animal death-rate has increased considerably in the area, from about 40 % to about 60 % per annum, and this is correlated with the increase in trawling operations in the area. The question is of paramount importance to the fishery of all nations working in the area and certainly the problem should be attacked by all available methods, age investigations, measurements, tagging, etc.

Rollefsen shows that the ratio females/males alters on the spawning grounds during the season, the percentage of females decreasing from 75 % to 40 %; this has also been observed in certain years on the spawning grounds of Iceland, and is probably a general rule for several species of fish.

Rollefsen's calculations of the size of the stock of "skrei" in 1937

and 1938 are of temporary importance, but should, however, be considered as valuable steps towards forecasting the yield of the fishery.

The oceanographic conditions in the area are dealt with by J. Eggvin, who shows clearly and concisely the importance of these investigations as a means of localizing the spawning cod and the Finmark cod. The systematic and continuous work in the area carried out for several years has shown important variations in the temperature distribution, showing that the deeper (Atlantic) water in the Vestfjord during 1933—36 had temperatures above the normal, in 1937 but nearly normal; the surface waters (down to about 150 m.) had considerably higher temperatures in 1937 than in the previous winter. In accordance with the temperature distribution, the cod occurred at a higher level than in the previous year. Echo-soundings were of great value for these investigations. As mentioned above, the Finmark area showed a strong influx of warm water along the coast, forcing the fish (and the fishermen) out into distant waters. The water transport eastwards through a special section off Finmarken was 843,000 m.^{3} per second, as against only 634,000 m.^{3} per second in 1936.

Å. Vedel Tåning.

H. Höglund. "Über die horizontale und vertikale Verteilung der Eier und Larven des Sprotts (*Clupea sprattus* L.) im Skagerak-Kattegatgebiet." Svenska Hydrogr.-Biolog. Komm. Skr., N.S., Biol., Bd. II, Nr. 3. Stockholm, 1938.

The investigation on the horizontal and vertical distribution of sprat eggs and larvae, reported in this paper, was undertaken from the Lysekil laboratory (mainly from May to July) in the years 1931 to 1934. A Hensen-net was used for the vertical hauls and a 1-metre closing ring-net for the horizontal hauls. Fish egg cruises in 1926 (May—June) and 1930 (June—July) had shown that sprat eggs were absent from the North Sea west of 7°E. Long., and only appeared at the entrance of the Skagerak. The results of 1931—1934 showed that the greatest concentration of eggs occurred in the neighbourhood of Skagen and that they decreased in number in a southerly direction in the Kattegat, and in a westerly direction towards the North Sea. The coast of Jutland between Hanstholm and Hirtshals was poor in eggs and they were almost absent from the Skagerak portion of the Norwegian deep water. The greatest numbers of eggs were found in water of 50 to 100 m. in depth. Text-figure 1 shows the chief spawning region as an inverted Y-shaped area embracing the Skaw. The author finds that the principal spawning grounds on the Swedish west coast lie outside the skerries, and he is of the opinion that eggs found in the fjords have mostly been carried into them by the currents, but that the Uddevalla fjord is an exception to this rule and constitutes a separate spawning area. He points out that his results do not agree with those of Ehrenbaum with respect to the usual depth of the water in regions where sprat eggs are abundant, and he also remarks that although the Jutland coast was considered by Sund as an important spawning area, he found it poor in sprat eggs.

It may be assumed that the vertical distribution of sprat eggs depends upon their specific gravity, and previous authors have held very diverse views on a possible alteration in specific gravity during development, in order to explain their observations on the differential vertical distribution of eggs in various stages of development. The author states that his

observations support the views, not only of those who maintain that the more advanced stages of development are commonest at the surface, but also of those who think that they are most numerous at the bottom, and likewise in mid-water! Some of his observations show an approximately equal distribution of developmental stages at all depths. He justifiably concludes that the vertical distribution of the different stages of development is exceedingly variable and is amenable to no codification whatever, but he discusses at some length the possible factors which may cause this variability.

It is well known that the eggs of many species of fish have a greater diameter in water of low salinity than in highly saline conditions. Thus eggs of the same species are found to have a greater size in the Baltic than in the North Sea, and likewise are larger in the eastern than in the western Baltic.

The author found that the mean diameter of sprat eggs usually decreased from the surface water to the bottom, whereas the salinity of the water increased. It is usually assumed that this variation in diameter in inverse ratio to the salinity of the water is an adaptation to enable the egg to float. The author points out that it is, therefore, an anomaly that eggs laid early in the spawning season should generally be larger than those spawned later, for the decrease in size here coincides with a diminution of specific gravity and viscosity of the water due to the rising temperature.

No special effort was made to collect sprat larvae, but a certain number were obtained with the eggs in the ring-net. It was found that the larvae were almost always commonest in the surface layers during the daytime.

The data are given in five tables and are fully illustrated by seven charts and six text-figures.

J. A. Robertson.

1) **R. M. Neill.** "The Food and Feeding of the Brown Trout (*Salmo trutta* L.) in Relation to the Organic Environment." Trans. Roy. Soc. Edinburgh, Vol. 59, Part 2, No. 18, pp. 481—520, 10 figs., 1 map. Edinburgh, 1937.

2) **K. R. Allen.** "Some Observations on the Biology of the Trout (*Salmo trutta*) in Windermere." Journ. Animal Ecol., Vol. 7, No. 2, pp. 333—49, London, 1938.

The natural history of the brown trout in the British Isles has attracted some attention in the past few years but our knowledge receives very valuable additions from these two papers. They differ greatly in scope and in method but they are to some extent complementary.

1) Neill has investigated one factor only, the food and feeding of the fish. For this purpose he selected a short length of the river Don in Scotland where trout were plentiful and conditions throughout the area studied approximately uniform. The whole programme of work was carried out between April and July. He measured such physical and chemical factors as appeared to be relevant, temperature, current, depth, size of particle on the river bed and the pH, alkaline reserve and carbon dioxide content of the water. He also gives a brief account of the flora.

His main object of study was naturally the fauna and it was investigated quantitatively by a new form of sampler which was very well adapted for the purpose. In all 13 samples, each from 1000 sq. cm. of river bed were taken and the data were compared with the stomach contents of 70 trout caught by the author on the same day as the faunistic samples

were taken. The results were extremely interesting. Statistical examination of the data showed that while there was in most instances a positive correlation between the frequency of occurrence of any one species in the fauna and in the stomach contents, the coefficient was smaller than would be expected if the intensity of utilization as food depended only on the abundance in the fauna. If, however, the habits of the food organisms are considered, it is found that some, e. g. *Simulium* pupae (which rise through the water in a bubble of air), are completely exposed to the depredations of trout, while others, e. g. Oligochaetes (burrowing in the substratum), are completely protected and if the "availability" of the various species be taken into account, then the difficulties of interpretation of the data disappear. Neill concludes, "The predatory relationship between the brown trout and its organic environment therefore is that the trout feeds on the whole range of animals present in whatever type of habitat it finds itself, to an extent dependent on their degree of accessibility and the extent of their representation in the fauna. This is sufficient to account for the nature of its stomach contents without invoking discrimination on the part of the fish."

This is an excellent paper in every way; the choice of a clearly defined problem, the careful and accurate methods of work, the treatment of the data (none wasted and none overstrained) and the soundness of the conclusions are models for other workers.

2) Allen's paper is considerably wider in scope. It deals with the age, growth, food, and numbers of trout in Windermere. Trout enter Lake Windermere from the streams in which they are bred at one, two, or three years of age, the faster growing migrating at an earlier age than the others. Fish in the lake live principally in the littoral region though some inhabit the deep waters and there is some interchange of populations between these habitats. They grow, on an average, 7 cm. a year and the oldest fish caught were 8 years old. Growth as shown by the scales varies seasonally, being most rapid in spring and early summer and slowing down in autumn and winter. There are, however, considerable individual variations and some fish continue to lay down wide annuli (indicating rapid growth) well into the winter and others begin rapid growth before the winter is over. The condition factor, the relation between length and weight, also varies, being highest when growth is fastest. The growth-rate deduced from the scales was checked by measurements of recaptured marked fish.

There is a very curious lacuna in this section. That the young fish are hatched in the streams is definitely stated but the fact that the mature fish are absent from the lake during the autumn is nowhere discussed. One would suppose that the absence of the spawning stock at one time and their return as spent fish would considerably influence the data, particularly those on the condition factor. Further it would be interesting to know the age at which the fish first spawn and whether thereafter they spawn annually.

Allen found that there was a seasonal variation in the nature of the food. His data may be summarized by saying that it consists of the permanent bottom fauna (Crustacea and molluscs) during the winter, insect larvae in the spring and surface food (insects) in the summer. The results are very similar to those obtained by Southern in his study of the food of trout in Lough Derg (Proc. Roy. Irish Acad., 42 B. 87—172. 1935). It is noteworthy that very few fish had been feeding on plankton, though since very few came from the open water of the lake this is not surprising, and

only a few of the larger had been feeding on other fish. Allen, unlike Neill, considers that there is evidence that trout definitely select their food. He says, "The nature of the food of a fish is controlled first by what is available and secondly by the behaviour of the fish" and does not apparently appreciate the factor which Neill found so important, the behaviour of the food organism.

Allen estimates the trout population of the littoral region to be 12,000 of which 50 % are in their third year and 25 % in their fourth, but the data on which this estimation is based are not clearly enough explained to allow its value to be assessed.

F. T. K. P.

A. C. Taft and **Leo Shapovalov**. "Homing Instinct and Straying among Steelhead Trout (*Salmo gairdnerii*) and Silver Salmon (*Oncorhynchus kirutch*)." Bureau Fish Conserv., Californian Div. Fish and Game, Vol. XXIV, No. 2, pp. 118—125. San Francisco, 1938.

The authors have marked young descending steelhead trout and silver salmon in two small creeks — Waddell Creek and Scott Creek — the mouths of which are about five miles apart on the Californian coast. One purpose of the experiment was to ascertain the accuracy of the homing instinct displayed by the two species, and an index was obtained by counting those which returned to one or other of the two creeks. There may have been wanderers to other streams, although none were found at the egg-taking station about 15 miles up the much larger San Lorenzo River, the mouth of which is about 15 miles south of Scott Creek. We are not told of the numbers marked, so that the proportion recaptured is unknown, but, of the 804 marked steelhead trout which were recaptured, only 15, or approximately 2 %, were retaken away from their original stream. Very few silver salmon were marked in Scott Creek, but, of the 168 recaptured from those marked in Waddell Creek, 35 or 21 % were retaken in the Scott Creek trap. No explanation is offered for the dissimilarity in the accuracy of return, although it is stated that the salmon marked from Waddell Creek have been recaptured as far as two hundred miles from the mouth of the creek. No mention is made of recaptures of marked steelhead trout at similar distances, and this may or may not be significant.

The very exact homing instinct of the steelhead trout is further confirmed by the recapture of fish marked as kelts (unlike the Pacific salmons, the steelhead trout do not die after spawning) and retaken as clean fish. Of 147 recaptures, only one was definitely known to stray from one creek to the other, although one marked fish was caught and released when ascending the "wrong" creek, and was later recaptured, before spawning, in the "right" creek; this fish had therefore imitated the known habits of some British sea trout, which temporarily ascend one water way before returning to another.

Further experiments were conducted in the Klamath River to ascertain the accuracy of return of steelhead trout to the particular tributary of a river in which they were marked as young fish. Of the 118 recaptures which were reported, only three adults were found in tributaries in which they were not marked as descending young fish. The tributaries were all situated more than 150 miles from the sea, and the mouths of all entering the main river within a distance of 15 miles of each other. They therefore

offered what appeared to be good chances for straying, but the fish showed a very exact homing instinct.

The experiments seem to have been planned and carried out to provide a fairly severe test of the homing instinct, and the presence of traps at all the essential points for taking fish for hatchery purposes ensured that a substantial proportion of the fish returning were captured. The results show that, in these waters, the steelhead trout have a homing instinct, the accuracy of which, for practical purposes, is complete. While the majority of silver salmon, on the other hand, similarly return to their native river from the ocean, a substantial proportion (roughly 20 %) failed to do so, and returned to another stream. Further experiments are required to confirm the steelhead results, to elucidate the apparent anomaly displayed by the silver salmon, and to test the accuracy of the return of the latter to their native tributaries in any given river system.

W. J. M. M.

F. A. Davidson and **J. Hutchinson.** "The Geographic Distribution and Environmental Limitations of the Pacific Salmon (Genus *Oncorhynchus*)." Bull. Bureau Fish. No. 26, Vol. XLVIII, pp. 667—692. Washington, 1938.

The authors give the distribution of the Pacific salmons from the Mackenzie River on the north coast of Canada to Monterey Bay in California, and from the Lena River in northern Sibiria down to the Amur River, with the pink and chum salmon extending as far as the Tumen River in northern Korea, together with corresponding distributions in the Island of Japan.

In addition to these native distributions, efforts have been made to extend the various species by the transplantation of eggs, starting in 1872, and extending right up to 1930. Practically all the eastern States of America, as well as the Atlantic side of Canada had, in the earliest days, heavy importations of eggs, and trials were made in other countries as far apart as Great Britain and the Argentine, France and Australia, Germany and Chile, not to mention Hawaii, Norway, Nicaragua, New Zealand, and Tasmania. Of all the transplantations, very few have been successful; Chinooks are reported to have been established in the St. John River, New Brunswick, and the Port Credit River, Ontario, while Coho or Sockeyes are reported to be running in the San Pedro River in Chile. European transplantations, and those in Australia and Tasmania were uniformly unsuccessful, and the only really well-established populations are in New Zealand. Even here the area of success is restricted to a limited area of the South Island, where sufficient Chinooks and Sockeyes are now said to exist to support a small commercial fishery.

The authors examine the conditions which favour the fish in their native habitats, and, somewhat surprisingly, give the temperature required for the young fish as being between 3° and 17° C. It is a little difficult to reconcile the lower limit with the arctic conditions which must exist in the majority of spawning streams, but possibly this limit applies to the young fish, and not to the eggs during the period of incubation. For the marine life, the suggested limits of mean surface temperature are between 5° and 15° C., although 0° and 20° are suggested as the extremes, with salinities from 33 to 35 ‰. A comparison between the various components of these environmental conditions, with similar figures from the areas of planting, serves to

explain the lack of success which attended most of the efforts, and the success which has attended the plantations in the restricted part of the South Island of New Zealand.

The paper forms an admirable summary of existing knowledge, and gathers together particulars of transplantations of eggs and fry which, at the best, are scattered very widely through the literature, and, at the worst, may be in danger of being lost. It further emphasizes the need for an accurate knowledge of the species dealt with and of the essential conditions in the proposed area of planting if there is to be a reasonable chance of success, and if time and money are not to be wasted. Competition between existing and imported species does not enter into the field of the authors of this paper, but it forms another most important element before colonization is attempted.

W. J. M. M.

A. E. J. Went. "Salmon of the River Shannon." Proc. Roy. Irish Acad., Vol. XLIV, Sect. B. No. 11, pp. 261—322, 26 diagrams, Pl. X. Dublin, 1938.

This paper, comprising a report on the examination of scales obtained from 1,709 salmon from the Shannon in 1927, is noteworthy for its meticulous thoroughness in the treatment of the material and as constituting a permanent record of the biological features of what may be presumed to be a typical season's run of salmon in the Shannon before the natural conditions on that river became substantially altered by the installation of the Shannon power scheme.

The material was obtained from two net fisheries at Lax Weir and Glyn, and from certain rod and line fisheries between O'Brien's Bridge and Killaloe. Comparison with the (confidential) returns of the catch at Lax Weir apparently satisfied the investigator that in the material undue importance was not given to any particular group of fish. It may be assumed, therefore, that this material constituted a representative percentage of the total catch. In addition there were 293 sets of scales of parr and smolts from different parts of the same river.

The most important part, commercially and in bulk, of the catch of salmon in the Shannon is referable to spring fish (the 2- and 3-winter groups) though numerically grilse constitute the highest percentage (34 %) of any group, and together with the small spring fish (the 2-winter group) comprise 66 % of the total number.

Grilse begin to run in May and continue until the end of July, the height of the run being in June. The average weight is rather more than 5¾ lb., with one notable specimen of 14½ lb.

The run of small spring fish is evident more or less throughout the fishing season, starting in February and continuing till July, being still evident a month later than the large spring fish (the 3-winter group), the run of which ends in June. The height of the run of spring fish, large and small, is in April. The average weight of the small spring fish is rather more than 14½ lb. (the largest being one of 25 lb.) and of the large spring fish not much below 28½ lb. (with the heaviest specimen weighing 49½ lb.).

Small summer fish (the 2+-winter group) are relatively unimportant — little more than 9 % of the total in number — the seasonal run being of short duration, covering as it does only two months, beginning in May and ending with June.

Large summer fish (the 3+-winter group) in the material amounted to only three in number and there were no more than twelve of the very large spring fish (the 4-winter group). The average weight of these latter was impressive at 40·94 lb., with two outstanding specimens of 52¾ lb. and 53 lb. respectively.

One of the most striking characteristics of these Shannon fish is the high C. F. Even in the grilse it was 42·2. It was highest among the large spring fish at 45·3 and lowest among the large and small summer fish at 41·2 and 41·8 respectively.

The percentage of fish that had spawned before (viz. 7·4 %) was rather higher than is usually supposed to be the case in most rivers. Of the 127 previous spawners 115 had spawned once and 12 had spawned twice. The majority of these had spawned as grilse (45) or small spring fish (49). There were, however, 33 that had spawned for the first time as large spring fish and 3 of these had spawned a second time. It is to be assumed that scale absorption in the Shannon fish is not commonly of an extreme type, so that the life periods in the scale records of a previous spawner can be identified with some degree of precision. The paper is silent on this point.

In the material examined females preponderated generally (68·2 %) except in the 2+-winter group, where the proportion was about equal and in the 3+- and 4-winter groups, where all but one (a large summer fish) were males. Even in the 3-winter group females constituted 60·7 % of the whole run.

As was to be expected, females greatly preponderated (74·5 %) among the previous spawners. The remarkable thing, however, was the high proportion of previously spawned males, of which no fewer than five had previously spawned twice.

Too much importance should, perhaps, not be attached to the proportions of the sexes as observed in a single season's run. From the evidence obtained in other rivers, the proportions appear to vary from year to year and though the fact may have an important bearing on the future stock resulting from any one season's spawning there are as yet insufficient data to warrant conclusions.

A considerable section of the paper deals with the growth of Shannon parr and smolts and the age of the latter at migration.

Over 98 % of the total catch is derived from one- and two-year-old smolts. The percentage of one-year-old smolts is high (nearly 24 %). Three-year-old smolts were too few in number to be of any statistical significance. Such as there were appear to have been limited to the grilse and small spring fish. The percentage of one-year-old smolts is highest among the spring fish — small and large. It increases with the age of the returning adults and also with the later running fish. In the 2+-winter group those derived from one-year-old smolts were of superior average length and weight than those from two-year-old smolts, while the reverse was the case in all the other groups.

The faster growing parr are the first to migrate, but no obvious correlation could be deduced between the rate of growth at this stage with the rate at which maturity is reached, that is to say, the period spent in the sea before return to fresh water, though there is an indication that the larger smolts give rise to larger adult fish.

In this connexion there is quite possibly some significance to be attached to the type of smolt at migration. According to the seasonal growth made in fresh water before migration, smolts can be divided into two types, viz.,

Type A, in which — as indicated on the scales — there is little or no growth subsequent to the preceding winter, and Type B, in which growth is definite and in some cases substantial. Both types are to be found in both one-year- and two-year-old smolts, though the percentage of Type A in the one-year-old smolts is very small. Type A smolts are longer at the end of the first and second winters of freshwater life than Type B. They also migrate earlier than Type B, the latter remaining in fresh water a little longer to make additional growth before migrating. This need for making additional growth immediately before migration is tentatively explained as a lag in the process of attaining a certain physiological condition which is necessary to bring about the impulse to migrate.

That somewhat obscure abstraction, physiological condition, has no doubt a good deal to answer for in the movements of salmon to and from the sea; but whether it can be revealed as a definite entity through a biological, physiological, psychological or mathematical approach remains to be seen.

T. E. P.-T.

J. R. Jones. "The Relative Toxicity of Salts of Lead, Zinc and Copper to the Stickleback (*Gasterosteus aculeatus* L.) and the Effect of Calcium on the Toxicity of Lead and Zinc Salts." Journ. Exper. Biol., Vol. 15, No. 3, pp. 394—407. London, 1938.

There are in the literature many discrepancies in the determinations by various workers of the toxicity of lead, zinc and copper salts to fishes. Some find them highly toxic, others do not. This extremely useful paper goes a long way towards explaining and reconciling these differences.

Jones, using the stickleback as the test animal, found that the lowest concentrations at which a toxic effect could be observed were one part of lead per ten million of water, three parts of zinc per ten million and two parts of copper per hundred million *when the solutions were made up with Aberystwyth tap water.* This water is very soft, containing only about one milligramme of calcium per litre and, so far as lead and zinc were concerned (copper was not apparently further investigated), he found that the addition of calcium salts to the water greatly decreased the toxicity. Thus he records that 50 milligrammes of calcium (as nitrate or chloride) was sufficient to annul the toxicity of a solution containing one part of lead or two parts of zinc per million of water. It seems reasonable to suppose that the discordant values for the lethal concentrations of these metals given by other workers are due to the varying hardness of the diluent water. Since the composition of the water has such an important effect it is unfortunate that Jones does not include in this paper a full analysis of Aberystwyth tap water.

These metals appear to exert their toxic effect by coagulating the mucus which covers the body and gills of the fish. This coagulated film eventually covers the gills and death occurs from asphyxiation. This paper records observations on the respiratory rate of fishes in lead and zinc solutions and, as would be expected, the rate rises rapidly to a value about three times the normal and this high rate is maintained until shortly before death. It was shown experimentally that the addition of calcium salts to mucus prevents its coagulation by lead or zinc salts. This is clearly the explanation of the reduction of toxicity in the presence of calcium salts, but the physics and chemistry of the process have not been worked out.

F. T. K. P.

F. T. K. Pentelow, R. W. Butcher and **J. Grindley.** "An Investigation of the Effects of Milk Wastes on the Bristol Avon". Min. of Agric. and Fish., Fish. Invest. Ser. I, Vol. IV, No. 1, pp. 76, 8 figs., 3 plates, 1 chart. London, 1938.

Die vorliegende Arbeit enthält die Ergebnisse eingehender Untersuchungen über den Einfluss der Abwasser einer Molkerei in Chippenham auf die Tier- und Pflanzenwelt des Bristol Avon, eines etwa 113 km. langen Flusses in der englischen Grafschaft Gloucester, der in den Bristol Kanal an der englischen Westküste mündet.

Die Beobachtungen beschränkten sich auf eine Strecke zwischen Langley Burrell, etwas oberhalb Chippenham und Melksham, das ungefähr 16 km. weiter stromabwärts liegt. Diese Strecke ist nicht schiffbar und nicht kanalisiert, hat somit noch ihren ursprünglichen Character bewahrt. Der Pflanzenwuchs ist reichlich an den seichten Stellen, doch nirgends so üppig, dass es nötig ist, die Bestände alljährlich zu schneiden.

Oberhalb der Fabrik war das Wasser nicht verunreinigt; Sauerstoff, Nitrate und Phosphate waren reichlich vorhanden. Die Algenflora und die niedere Tierwelt stimmten im grossen und ganzen mit denen der übrigen Ca-reichen Flüsse Südenglands überein.

Die Molkerei entsandte nur Spül- und Kondensorwasser, beide Milch in geringen Mengen enthaltend, in den Vorfluter, wodurch zunächst eine erhöhte Trübung des Flusswassers sowie ein Aufblühen gewisser Abwasserpilze, namentlich *Sphaerotilus natans*, hervorgerufen wurde. Es bildete sich des weiteren eine Schicht schwarzen Schlicks auf dem Boden, der Sauerstoffgehalt des Wassers nahm ab, *Asellus* und Hirudineen waren zahlreich. Die städtischen Abwasser, die etwa 1·5 km. unterhalb der Molkerei in den Fluss geraten, erzeugten eine erhöhte Verschlechterung des Wassers, waren jedoch nicht besonders schädlich; im Gegenteil, es zeigte sich von dort an eine fortgesetzte Entfaltung der Algenvegetation. Wiederum 1·5 km. weiter stromabwärts wurde der Zustand schon bedeutend besser: der Algenwuchs wurde allmählich bedeutungsloser und das Verhältnis der Aselli und Hirudineen zu den übrigen Komponenten der Fauna war auffallend geringer geworden.

Seitdem nun die Molkerei dazu übergegangen ist, ihre Abwasser durch die städtischen Abflussröhre zu entfernen, ist eine allgemeine Besserung eingetreten; die Zahl der Crustaceen nahm bedeutend zu und *Simulium*-Larven erschienen an Stellen, wo sie früher fehlten.

Die Arbeit enthält viele Diagramme und Tabellen über die beobachteten Pflanzen und Tiere, doch leider fehlen bei verschiedenen Insektenlarven die zugehörigen Spezies-Namen.

H. C. R.

P. H. T. Hartley and **G. M. Spooner: L. H. N. Cooper** and **A. Milne: A. Milne.** "The Ecology of the Tamar Estuary. I. Introduction": "II. Under-water Illumination": "III. Salinity and Temperature Conditions in the lower Estuary". Journ. Mar. Biol. Assoc., Vol. XXII, No. 2, pp. 501—508, pl. XVIII: pp. 509—528, figs. 1—6: pp. 529—542, figs. 1—5. Cambridge, 1938.

Wie aus der "Einleitung" hervorgeht, ist von den englischen Untersuchern eine umfassende Schilderung der ökologischen Verhältnisse des Tamar-Aestuars (Hamoaze) geplant. Das erste der drei bis jetzt erschienenen,

obenerwähnten Hefte enthält zunächst verschiedene Angaben über die geophysischen und meteorologischen Verhältnisse der durchforschten Strecke (Bodenbeschaffenheit, Tiefe, Ausdehnung der Gezeitenzone, Regenfall), einige Notizen über die Bedeutung menschlicher Eingriffe (Fischerei, keine schädliche Wasserverunreinigungen!) und schliesslich eine kurze Übersicht über frühere biologischen Arbeiten im Gebiet, die allerdings vorwiegend die Fauna zum Gegenstand hatten.

Die zweite Abhandlung bringt die Ergebnisse eingehender Untersuchungen über die sowohl im Sommer wie im Winter für Pflanzen verfügbaren Lichtmengen an den Ufern und auf den im Strom verankerten Bojen. Es wurde ein Pulfrich Photometer von Zeiss mit acht Spektralfiltern benutzt. Über die ganze Ausdehnung des sichtbaren Spektrums waren die Auslöschungskoeffizienten in der Hamoaze immer höher als im englischen Kanal. Besonders erwähnenswert ist, dass, im Gegensatz zum offenen Meer, rotes Licht ebensogut oder sogar besser eindringt als grünes, während Blau sehr schnell verschwindet.

Das dritte Heft enthält Daten über den Salzgehalt, die Temperatur und den Wasserstoffexponent des Wassers auf der untersuchten Strecke. Wie zu erwarten war, zeigten sich die Schwankungen im Salzgehalt der Oberfläche als sehr erheblich. Aus zwei Beobachtungsserien zwischen Saltash und Neal-Point, also im oberen Teil des Aestuars und etwas unterhalb der Mündung des Tavy, geht hervor, dass hier der Oberflächensalzgehalt in der Zeit von Niedrigwasser bis Hochwasser am 24. Mai 1937 von 15 $^0/_{00}$ bis zu 29 $^0/_{00}$ stieg, am 3. Juni desselben Jahres in der entgegengesetzten Periode von 31 $^0/_{00}$ bis auf 26 $^0/_{00}$ hinabsank. Die Variationen am Boden waren selbstverständlich viel geringer; die gefundenen Werte liegen hier zwischen 24 und 31 $^0/_{00}$, bezw. 32 und 29 $^0/_{00}$. (Man vergleiche die Querschnitte S. 531). Auch aus den zahlreichen, an anderen Stationen ausgeführten Bestimmungen geht hervor, dass das untersuchte Gebiet einen durchweg polyhalinen, zum Teil sogar einen rein marinen Character hat.

Die Angaben über die Temperatur des Oberflächenwassers beziehen sich hauptsächlich auf zwei Beobachtungsserien: eine im unteren Teil des Aestuars (Breakwater), die andere im oberen (Saltash). Dieselben wurden mit zweiwöchentlichen Zwischenräumen vom Januar bis Juni 1937 angestellt und lieferten einen neuen Beweis für die — übrigens schon in vielen anderen Flussmündungen beobachtete — Tatsache, dass die Schwankungen sowie der Unterschied zwischen Maximum- und Minimumtemperaturen in der Nähe des Meeres bedeutend geringer sind als mehr stromaufwärts. Dass das Wasser ausgesprochen alkalisch war, pH am 27. April 1937 im oberen, mesohalinen Abschnitt = 7·54, im Polyhalinikum = 8·15—8·23, ist schliesslich ebenfalls nicht sehr befremdend.

Hoffentlich lassen die faunistischen und floristischen Ergebnisse der Untersuchungen in diesem interessanten Gebiet nicht allzulange auf sich warten.

H. C. R.

Various. "Neue Untersuchungen über die chinesische Wollhandkrabbe in Europa." Mitt. Hamburg. Zool. Mus. u. Inst., Bd. XLVII, S. 1—171, 1 Titelbild, 49 Abb. Hamburg, 1938. (The papers issued separately at various dates between June 1937 and March 1938).

This volume of papers by members of the staff of the Hamburg Zoological Museum and Institute forms a supplement to the Monograph on the Chinese Mitten Crab published in 1933 by Peters, Panning, and

Schnakenbeck. The extension of its range in Europe is traced down to the end of 1935 and the results of further investigations into its life history and habits and into the methods of combating it and of utilizing it for various purposes are dealt with. It is not possible here to give a full analysis of the results and only a few of the more interesting points are mentioned below, but it can be said that this alien immigrant is well on the way to become one of the most fully investigated of European Invertebrates.

In the first paper Dr. Peters has collected all records of the occurrence of the Mitten Crab between 1933 and 1935. In the latter year its area of distribution extended from Viborg, in the Gulf of Finland, to the Thames, where, however, there are no further records since a single specimen was found at Chelsea in 1933. Dr. Peters points out the striking contrast between the conditions in the area of the southern North Sea and those in the Baltic. In the former area there has been a rapid increase in the abundance of the crab, especially in the German rivers, accompanied by a comparatively slow coastwise extension of its range. In the Baltic there has been a very rapid extension in the area from which the crab has been recorded but little evident increase in its abundance. There is no evidence that the Mitten Crab breeds in the Baltic where the salinity in the neighbourhood of the river-mouths nowhere reaches the 15 $^0/_{00}$ which is the minimum for the hatching of the eggs. To the west, there is some evidence that temperature is the limiting factor and the estuarine waters my be too warm to allow the crab to spread beyond the Franco-Belgian border. The Elbe and the Weser are the most heavily infested rivers and Dr. Peters gives striking figures showing the incredible abundance of the crabs. In the harbour of Cuxhaven in June 1936 at low tide the bottom was seen in places to be carpeted with a continuous layer of crabs piled one upon another. In many districts, however, a diminution in abundance was observed in 1935 due, it is believed, to the energetic measures taken for the trapping and destruction of the unwelcome invaders.

Dr. Panning reports on the results of marking experiments designed to trace the migration of the young crabs from the estuaries into fresh water and the subsequent descent of the maturing individuals. The young hatched in the late spring or early summer remain for about 18 months in the tidal reaches and mostly begin their ascent of the rivers in their second winter when they are at least 9 mm. long. The rate of travel averages about 1 to 3 kilometres per day.

How long they remain in the fresh water is not known. The large crabs (up to 50 mm. long), with ripening gonads, begin their downstream migration towards the end of August or the beginning of September, the movement starting simultaneously in different localities. They seem to travel without pausing, unlike the ascending young, and to cover the surprising distance of 8 to 12 kilometres per day. Pairing and egg-laying take place in the estuaries where the salinity is not less than 15 $^0/_{00}$.

Papers by Panning and by K. Schubert on rate of growth, moulting, and year-classes agree in general results. A length of 25 mm. is reached in the second year and 36—40 mm. in the third. Individuals of 50 mm. are five years old. Some may become mature in the third year but the spawning swarms are mostly in their 4th and 5th years.

Dr. Thiel has investigated the feeding habits with special reference to the alleged damage to fisheries. He finds that the crabs do not attack living fish. Only 3 $^0/_0$ out of nearly 3000 individuals contained fish remains in the stomach, no doubt from dead fish found on the shore. In the main the

crabs are vegetable feeders but some animal food seems to be essential for them. They may be serious competitors with herbivorous fishes.

Dr. Peters has also studied the reproduction. He finds that in special circumstances the females may breed more than once but that the majority appear to die after spawning.

Dr. Peters and Herr Hoppe report on the various devices that have been found effective for catching the crabs, among which are traps and pitfalls placed so as to catch them when travelling overland to surmount weirs and other obstructions. The utilization of the large quantities captured has been the subject of many experiments. In the fresh state they can be used as food for poultry and for silver foxes and the like. The manufacture of a kind of fish meal is being tried and appears to afford a satisfactory food for poultry and pigs although its high content of indigestible matter limits the extent to which it can replace other feeding-stuffs. So far, however, the prices obtained represent no more than a deduction from the expense of catching.

W. T. C.

Current Bibliography.

Prepared by the Editor with the assistance of Miss Thursby-Pelham.

NOTE. The scope of the Bibliography is limited in the main to the area covered by the Council's activities, but there are included papers of general interest relating to other areas in North Temperate and Arctic regions and exceptionally elsewhere. Limnological references are not as a rule given, but papers relating to brackish waters and to salmon and freshwater fish studied by the Council are included.

Subscribers and those on the distribution list will receive regularly upon application to the Administrative Secretary copies of the Bibliography printed on one side of the page only, for use in making up card indices.

The Editor will be glad to be advised of emendations and additions to the Bibliography.

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